

IMPORTANCE, DRIVERS AND CONSERVATION OF WILD BEES FOR APPLE
POLLINATION

A Dissertation

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IMPORTANCE, DRIVERS AND CONSERVATION OF WILD BEES FOR APPLE POLLINATION

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My dissertation used a multi-disciplinary approach to address the following questions: In the face of global honey bee declines and increasing demands for insect pollination can wild bees ensure adequate pollination? If so, how do we conserve these bees and services? Through pollination experiments in 2010 and bee inventories in 19 central New York orchards in 2011 and 2012, two dominant native bee groups, *Andrena* subspecies *Melandrena* and *Bombus*, were found to be as effective pollinators as honey bees (*Apis mellifera* L.), per-visit. Pollinator importance across orchards was driven by relative abundance, and was low for native bees compared to honey bees study-wide. The roles of pest management and natural areas surrounding orchards as drivers of wild bee abundance and species richness within 19 surveyed orchards were investigated. Early fungicide and late insecticide applications had strong negative effects on wild bees. Conversely, increasing natural areas in the landscape weakened pesticide effects. Combined increases in chemical inputs and land simplification resulting from agricultural intensification, therefore, pose a risk to wild bees and their pollination services. A holistic approach to balancing costs and benefits of pest management decisions is needed. To inform future wild pollinator conservation and extension to this end, grower perceptions and attitudes of wild pollinators in New

York and Pennsylvania were assessed between 2009 and 2012. Growers had high appreciation for wild pollinators, an openness to rely more on naturally occurring bees, and willingness to adopt low-cost, bee-friendly management practices. At the same time, growers reported measurable uncertainty about the effectiveness of alternative pollinators. This uncertainty was the primary obstacle for growers to consider actively managing orchards for wild bees. In sum, wild bees provide important pollination services for the New York apple industry. Wild bee pollination could fill pollination gaps left by declining honey bees, but only where orchards and the surrounding landscape are managed in a manner that supports wild bee abundance. Grower perceptions of wild pollinators are generally positive, but encouraging growers to explicitly integrate wild bees into their pollination strategy requires extension programs that inform growers of wild pollinator efficiencies and provide guidance in implementing pollinator-friendly management practices.

BIOGRAPHICAL SKETCH

Mia Park is following through on a career that began as a child exploring a fascination with nature. Inquisitive and observant from a young age, insects were the wildlife in Mia's urban backyard. Completing her dissertation at Cornell University is the icing on the cake of previous layers of study: Bachelors of Science in Environmental Studies and of Arts in French from University of California, Davis, 1999, and a Master of Science in Natural Resources from Cornell University, 2006. Mia starts a new position as assistant professor in the Humanities and Integrated Studies Program at University of North Dakota this fall.

Mia's research is motivated by a passion for insect conservation and a commitment to informing wise management of natural resources with sound science. Mia has been active in extension and outreach, including producing a well-received handbook entitled, "Wild Pollinators of Eastern Apple Orchards and How to Conserve Them." Mia has received several research awards and fellowships, including a College of Agriculture and Life Sciences Land Grant Extension Fellow. For the Entomological Society of America, she has served as a national meeting volunteer, moderator, program symposium co-organizer and journal reviewer. Service in her community includes supporting events that encourage women in science and that engender appreciation of insects.

At the bottom of all this study and activity, Mia simply loves insects because of the boundless sense of discovery that comes from studying them.

To my little family.

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CHAPTER 1

POLLINATOR EFFECTIVENESS AND IMPORTANCE OF NATIVE *BOMBUS* AND *ANDRENA* (*MELANDRENA*) COMPARED TO HONEY BEES IN EASTERN APPLE ORCHARDS

Abstract

Recent declines in honey bee health and increasing demand for pollination services highlight a need to optimize pollination by wild bees in agriculture. Apple requires insect pollination, and growers rent increasingly expensive honey bees to ensure adequate pollination. Apple is visited by a diverse and abundant wild bee community in New York State; however, an assessment of the pollination services contributed by wild bees is lacking. The calculation of “Pollinator importance”, as the product of pollinator effectiveness and relative abundance, provided a framework to experimentally quantify the contribution of native bees to apple yield and quality. We compared pollinator effectiveness and importance of two common native apple visitors, large mining bees (*Andrena* in subgenus *Melandrena*) and bumble bees (*Bombus* spp.) to that of honey bees (*Apis mellifera*). To provide a meaningful measure of per-visit effectiveness, we translated per-visit pollen deposition to fruit and seed set, by experimentally developing functional relationships between pollen deposition and these measures of reproductive success. Relative abundance was surveyed in orchards across central New York in 2011 and 2012. *Melandrena* and *Bombus* visitors directly contacted the stigma more frequently than *Apis* and, as a result, deposited more pollen per visit. After accounting for resulting fruit and seed set, *Melandrena* and *Bombus* were found to be as effective pollinators as honey bees per-visit, but not better. Pollinator importance at the orchard level, therefore, varied

with relative abundance across farms. For the entire study region, the combined pollinator importance of *Melandrena* and *Bombus* was only 30% that of honey bees. Our results suggest that future regional pollinator gaps cannot be filled by one or two native pollinators alone, but will require entire wild bee communities, and will only occur when conditions in and around orchards support their abundance.

Introduction

Animal pollination is essential for sexual reproduction of many wild flowering plants and agricultural crops. At least, 35% of global crop production benefits from animal pollination (Klein et al. 2007). Bees are by far the most important pollinators in agricultural settings and contribute between \$5.7 to \$19 billion per year to the United States economy (Levin 1983, Robinson et al. 1989, Southwick and Southwick 1992, Morse and Calderone 2000, Losey and Vaughan 2006) and \$217 billion per year globally (Gallai et al. 2009).

The most widely-used bee for crop pollination is the European honey bee, *Apis mellifera*. Honey bees are ideal pollinators in many crop systems, especially in large scale, highly disturbed agroecosystems. Colonies, each producing thousands of foraging workers, can be moved into fields during the flowering period. However, steady declines in honey bee populations over the past 50 years (National Research Council 2007), and significant colony losses due to “Colony Collapse Disorder” (Oldroyd 2007, vanEngelsdorp et al. 2009), have resulted in increased hive rental fees and supply shortages for growers. Relying on a single pollinator species for food production may not only be risky (Winfrey 2008), it may also be inefficient: fruit set of a suite of global crops consistently increased with wild bee but not honey bee abundance (Garibaldi et al. 2013). While the mechanisms for such differences are unclear, these results suggest that wild bees may compensate for continued honey bee

losses. Quantifying contributions of specific pollinators to a crop involves detailed pollination study, ideally, over multiple years and sites, but is a useful approach to assessing whether native bees can fill a potential pollinator gap and can focus management for the most important alternative pollinators.

Pollinator importance is one metric of the relative contribution of pollinators to crop production at the field or orchard level. This metric is estimated by assessing, in combination, per-visit effectiveness of floral visitors and their visitation frequency (Olsen 1996, Vázquez et al. 2005). Stigmatic pollen deposition is the most frequently used proxy for per-visit reproductive success (Ne'eman et al. 2010). Differences in pollen deposition can be attributed to pollinator taxonomic identity, morphology, sex, body size and flower handling behavior (e.g., (Tepedino 1981, Cane et al. 1996, Thomson and Goodell 2001, Javorek et al. 2002). The use of pollen deposition as a proxy for pollinator effectiveness is advantageous in that it isolates pollinator quality in the presence of post-pollination processes, such as maternal resource competition, pollen tube competition, and fruit or seed loss due to herbivory, all of which can obscure differences in efficiencies among pollinators (Cane and Schiffhauer 2003).

Pollen loads, however, do not always translate directly to probability of fruit set, seed set or fruit size, typical measures of reproductive success (Cane and Schiffhauer 2003). The relationship likely follows a nonlinear saturation function with a minimum threshold of pollen transfer needed to initiate fruit and with a maximum threshold for optimal reproductive success (Harder and Thomson 1989). For example, a pollinator that deposits twice the pollen needed for fruit set is not a better pollinator than one that consistently deposits the minimum pollen requirement (Cane and Schiffhauer 2003). For self-incompatible plant species, the use of pollen loads is further complicated by an observer's inability to distinguish self from cross-pollen (Snow 1982). Such issues can be remedied, however, if relationships between

stigmatic pollen load and fruiting response are established (Cane and Schiffhauer 2003).

Apple (*Malus pumila* Mill: Rosaceae) is an economically important crop worldwide, and dominates growing regions in northeastern and northwestern United States. Apple is self-incompatible and requires cross-pollination by insects (McGregor 1976, Free 1993). While renting honey bees to pollinate this mass blooming crop is commonplace in North America, surveys of orchards over the past century indicate that apple flowers commonly are visited by wild, native bees, particularly species in the genera *Andrena*, *Bombus*, *Halictus*, *Lasioglossum*, and *Osmia* (Hutson 1926, Brittain 1933, 1935, Phillips 1933, Loken 1956, Gardner and Ascher 2006, Park et al. 2010, Watson et al. 2011). A number of studies indicate that native bees may be better apple pollinators on a per-visit basis than honey bees. Native bee species have been shown to carry more pollen (Kendall and Solomon 1973), to carry more compatible pollen (Kendall 1973), to transfer pollen at a higher rate (Thomson and Goodell 2001), to yield higher fruit set per visit (Vicens and Bosch 2000), and to show a stronger preference for *Malus* flowers than do honey bees (Kendall & Solomon 1973, Johnson 1984, Vicens & Bosch 2000a). Aside from research on mason bees (*Osmia* spp.; (Vicens and Bosch 2000, Sheffield 2014), however, previous studies have not documented contributions of specific wild pollinators to apple's reproductive success (fruit set, seed set and fruit quality), nor have previous studies attempted to quantify the regional importance of native bees in apple pollination (for exception, see Brittain 1933).

Here we experimentally compared contributions of honey bees and two native bee groups, *Bombus* and large *Andrena* in the subgenus *Melandrena*, to apple pollination in New York State, using pollinator importance as our framework. We measured pollen deposition to compare per-visit effectiveness among bee groups. To

account for apple's self-incompatibility and high rates of natural and managed fruit abortion, we developed functional relationships between pollen deposition and reproductive success to provide more reliable measures of per-visit pollinator quality. Relative abundance was captured at 19 total farms across central New York State. Specifically, we asked whether *Bombus* and *Andrena* were higher quality pollinators than honey bees based on per-visit reproductive success; and quantified their relative importance for apple pollination in the region.

Materials and Methods

Study Site and Organisms. Rates of per-visit pollen deposition by free flying pollinators were observed in May 2010 at Cornell University's experimental orchard (CU), Ithaca, New York (lat:42.444808°, lon:-76.462345°). In spring 2011, we developed functional relationships between per-visit pollen deposition and reproductive success at CU and at a commercial orchard near Berwick, Nova Scotia (NS, lat: 44.98396, lon: -64.78479). To eliminate for differences in flower morphology and pollinator behavior among varieties pollination experiments were conducted on a single variety: 'Honeycrisp' apple (*Malus pumila*, Mill). At both orchards, experiments were conducted on two rows of Honeycrisp trees, grown on dwarf rootstock. The spatial arrangement of tree rows was similar at study orchards in terms of tree and row spacing; experimental rows were flanked on either side by co-blooming varieties. Bee surveys in 16 and 19 orchards in 2011 and 2012, respectively, throughout central New York provided relative abundance data used to scale up per-visit effectiveness to pollinator importance at the orchard level.

Apple is self-incompatible and requires cross-pollination by insects (McGregor 1976, Free 1993). Since commercial varieties are clonally produced, flowers must receive pollen from other varieties or crabapples (i.e., pollinizers) for fertilization to

occur. Apple's determinate flowers typically grow in clusters of 5 to 6, with the primary or 'King' blossom producing the largest fruit. Five stigmas, fused two thirds down the style, are positioned distal to ring of 20-25 anthers. Each stigma leads to a carpel, where the ovaries are located and bear 2 ovules. Most apple cultivars, therefore, set a maximum of 10 seeds. Stigmas are receptive for only 1-3 days.

To produce a commercially viable crop, apple requires 5-10% of blossoms to set fruit (Brittain 1933). If fruit set is high, apple trees naturally abort the weakest fruit and will not yield well the following year, a phenomenon called biennial bearing. Fruit quality, in terms of size and shape, is also affected by insect pollination, as low seed set and empty carpels can result in small or asymmetric fruit with lower market value (Sheffield 2014, Garratt et al. 2014). For pollination, it is common practice for apple growers to bring honey bee (*Apis mellifera*, hereafter referred to as *Apis*) hives into orchards during bloom to ensure adequate fruit set (hives were present at both our study sites). The advantage of *Apis* is their sheer number and not necessarily their pollinator quality (Westerkamp 1991). If fruit set is deemed too high, growers typically chemically stress trees, a process called thinning, to abort additional fruit to avoid biennial bearing (Wertheim 2000).

Apple blossoms produce abundant nectar and pollen, and because of their open morphology apple can be visited by a wide variety of pollinators (McGregor 1976). Since 2009, 100 species of wild bees have been surveyed on apple blossoms in central New York State. Wild bee communities are most abundant and diverse in orchards that minimize pesticide use and are nestled in landscapes covered with 30% or more natural areas (Park et al. *in review*). Numerically, the dominant native bees surveyed in orchards are the solitary, mining bees (genus *Andrena*) and bumble bees (genus *Bombus*, Figure 1.1). Among *Andrena*, the large mining bees in the subgenus *Melandrena* (hereafter referred to as *Melandrena*) have potential to be important apple

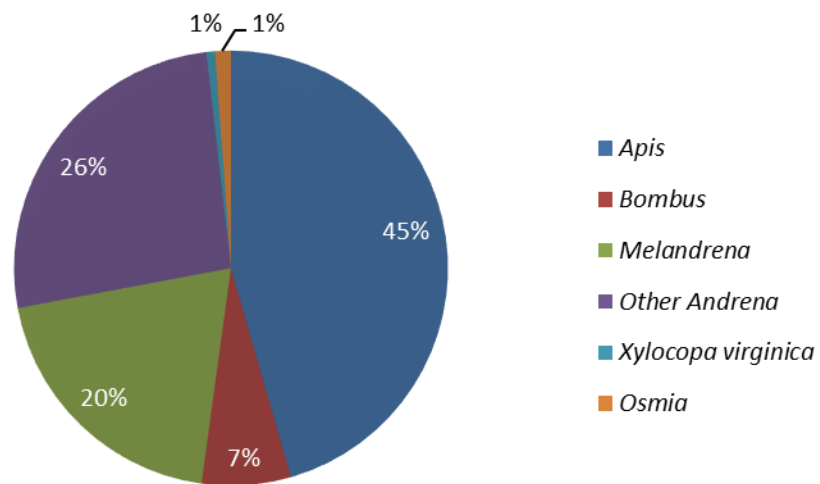


Figure 1.1. Relative abundance of major bee groups visiting apple, collected from 2009-2013 from orchards in the central New York study region.

pollinators due to their large honey-bee size, early spring phenology, and abundance in eastern orchards (Brittain 1933, Phillips 1933, Gardner and Ascher 2006, Park et al. 2010, Watson et al. 2011). *Melandrena* may prefer apple (Gardner and Ascher 2006), as andrenids carry large quantities of apple pollen on their bodies (Kendall and Solomon 1973). Andrenids also store their pollen dry in dense and specialized scopal hairs starting from the propodeum and base of hind legs on the trochanters to the hind tibiae, which can be more readily transferred to stigmas (Thorp 2000). In contrast, *Apis* and *Bombus* store moistened pollen in pollen baskets, called corbiculae, on the hind tibiae (Figure 1.2d). Corbicular pollen is generally considered unavailable for pollination (Westerkamp 1991).

Bombus is already considered a good apple pollinator by growers for its ability to forage in temperatures too low for other bees to be active (Brittain 1935). *Bombus* also transfers more pollen than honey bees while visiting apple, by handling flowers from the top or ‘topworking’ compared to honey bee ‘sideworking’ (Figures 1.2a, b). Sideworking describes foraging for nectar, by standing on a petal and probing through stamen filaments and avoiding contact with stigmas (Thomson and Goodell, 2001). Sideworking is a well-documented behavior for honey bees (McGregor 1976 and references therein) that can reduce per-visit seed set and fruit development (Robinson and Fell 1981). To our knowledge, nobody has yet documented *Melandrena*’s tendency to sidework. Despite indirect evidence that both *Melandrena* and *Bombus* are as good, if not better, pollinators than *Apis*, previous work has not assessed their contributions to apple’s reproductive success (i.e., fruit and seed set; see Table 1.1 for more information on bee life histories).

Figure 1.2. Foraging behaviors and pollen placement of bees visiting apple in 2010 at Cornell University Orchards: topworking *Melandrena* (a), sideworking *Apis* (b), pollen stored in large scopal hairs along the entire back leg of a topworking *Melandrena* (c), corbicular pollen basket on hind leg of topworking *Apis* (d), topworking *Xylocopa virginica* probing for nectar (e), topworking small *Andrena* with pollen in scopa. Photos taken by Kent Loeffler.

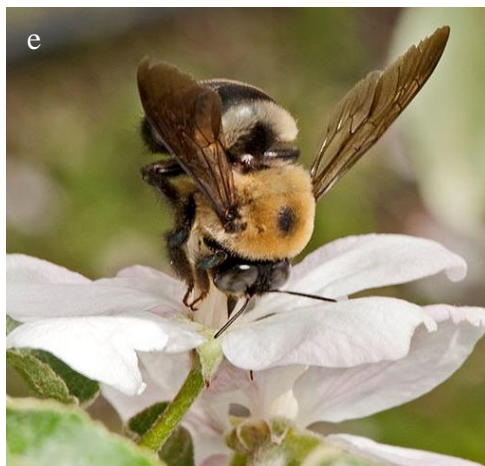
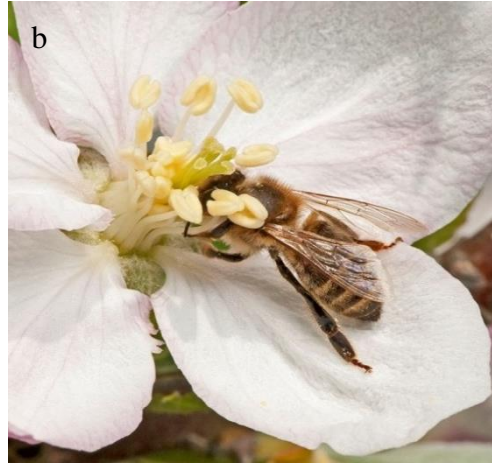


Figure 1.2

Table 1.1. Life history information for bee groups.

	<i>Apis mellifera</i>	<i>Melandrena</i>	<i>Bombus</i>
Sociality	Eusocial	Solitary	Eusocial
Nesting	Hive in cavity	Ground	Hive in cavity
Female length (mm)	5-15	10-15	17-21
Pollen placement	Corbicula on hind tibia	Hind trochanteral floccus; scopa on femur, tibia and propodeum	Corbicula on hind tibia
Dominant species	<i>Apis mellifera</i>	<i>Andrena vicina</i> <i>A. regularis</i> <i>A. dunningi</i> <i>A. carlini</i>	<i>B. impatiens</i> <i>B. ternarius</i>

Relative abundance. Standardized bee surveys were conducted during apple bloom in spring 2011 and 2012. All bees observed on apple blossoms were net-collected along transects that spanned 50 m of two tree rows for 15 minutes. Collecting occurred during peak bee activity between 10:00 and 15:00 hr, with temperatures above 16⁰ C and enough sunlight to cast a shadow. Because transect number varied by farm, for each bee group we calculated average abundance per transect at each farm per year. We divided the average abundance per transect for each bee group by the total average abundance per transect of all three bee groups included in the study to calculate relative abundances of our focal bees at each farm.

Free-foraging pollen deposition and behavior. To compare pollinator per-visit effectiveness of *Melandrena* and *Bombus* to that of *Apis*, we quantified pollen deposition from a single visit (Thomson & Goodell, 2001). A few days prior to opening, apple flowers in the balloon stage were emasculated and bagged to prevent contamination from self-pollen and other insects, respectively. We “interviewed” foraging bees between 09:00 and 19:00 on fair days, by offering them open, viable flowers attached to the tip of a 0.5-m rod. We used flowers that had produced nectar, as we found it difficult to get a bee to visit otherwise, and had receptive stigmas (which had not turned brown). A legitimate visit was determined by active foraging or direct contact with the stigma. Each visit was timed using a stopwatch and the following response variables were recorded: length of visit, reward sought (pollen, nectar collection or mixed), approach (top, side or mixed), and presence of pollen loads. After a visit, stigmas were removed with clean forceps at the point where they fuse, and placed in a drop of melted glycerin jelly tinted with basic fuchsin on a microslide. We applied firm pressure to the top of a cover slip to squash the stigma and distribute the pollen grains into a monolayer. Clear nail polish was used to seal

the cover slip edges. All pollen grains were counted at 200× magnification under a Leitz compound microscope. Due to the difficulty of distinguishing among Rosaceae pollen, we categorized pollen as Rosaceae or other, with the assumption that Rosaceae pollen is largely apple since bees were foraging on apple trees.

Without anthers, emasculated flowers were morphologically distinct from un-manipulated apple blossoms. In order to assess natural differences in foraging behavior, we observed bees naturally foraging within 15-min increments throughout days when bees were interviewed. Each bee was followed as long as it remained within sight. In 2010, we recorded the following for each foraging “bout”: bee taxonomic identity, reward sought, approach, and time at each flower. We conducted similar observations in 2011 for one afternoon, to record additional data on visitation rates, but only on *Melandrena* and *Apis*. Total bout duration (how long we could follow the bee as a proxy for cross-row movement), number of flowers visited per minute, and number of trees visited per minute were recorded. To minimize influences of external factors such as time of day or temperature, we alternated observations among the bee groups.

Manual applications of bees. To develop functional relationships between per-visit pollen deposition and apple reproductive success, in May 2011, we applied pollinators to emasculated, virgin Honeycrisp blossoms that remained on the tree, so they could develop into fruit. Flowers that received hand-applied, 100% cross pollen and flowers that never received pollen served as positive and negative controls, respectively. At NS, we added a pollen placement treatment to see if pollen stored within the scopa and on the bee thorax differed in viability, as scopal pollen is considered unavailable for pollination (Westerkamp 1997). As described for interview flowers, experimental blossoms were bagged before opening to prevent

insect visits and emasculated prior to the experiment. At CU, poor weather conditions limited availability of viable blossoms, so we randomly assigned treatments to blossoms. At NS, we performed a complete-block design where 29 trees were systematically selected among two rows. For each tree, eight flower clusters were randomly assigned to each treatment (2 controls, 3 bee x 2 pollen placement treatments).

To apply bees to flowers, foraging bees within experimental rows were individually collected in clean, glass vials. Once a bee was immobilized on ice, the bee was held by clean forceps and the underside of the thorax was applied gently, but directly, to stigmas for 5 seconds. The lateral, exterior edge of one scopa was similarly applied to stigmas to another flower cluster. For *Melandrena*, scopa on the tibia consisting of dense, long hairs that store dry pollen, were applied, whereas for *Apis* and *Bombus*, corbiculae that hold wet pollen together with nectar on the hind tibia were applied. To control for competition effects among fruits, clusters were thinned to just the one experimental blossom. Crab apple pollen for positive controls was collected up to 48 hours prior to application, by placing anthers under a desk lamp in an open petri dish to dehisce. Viability of the pollen was confirmed by staining with lactophenol-1% aniline blue (Kearns and Inouye 1993). All flowers were rebagged after each treatment to ensure fertilization and seed set resulted from treatments only.

We recorded per-visit pollen deposition, by removing stigmas from treated flowers 48 hr after pollination, mounting and counting them on microslides as we had done the previous year (described above). Waiting 48 hr ensured that fertilization had already occurred before stigma removal. We removed bags at this point to allow for full fruit development. A week after pollination, fruit set was recorded. Apple fruitlets were collected two weeks after pollination, just before chemical thinning. Fruitlet size, number of viable seeds, and number of carpels with, at least, one developing seed

were recorded for each fruit. For CU fruit, we measured fruit size as the diameter with a digital caliper and identified viable seeds as those that were actively growing (i.e., larger and fully inflated vs. small and shriveled). We were unable to similarly process NS fruitlets, as they were held up in international customs and arrived shriveled. We recorded fruit size as dry weight (g) and identified seed viability by length. We measured the length of all seeds in mm using a ruler at 10x on a Leitz stereoscope. A subsample of seeds was also weighed, showing a strong correlation between length and mass (Figure 1.3). Seeds displayed a bimodal distribution, which guided a conservative cutoff length for viable seeds at 1.4 mm. In fall 2011, we verified that this was a reasonable cutoff size for seed viability, by haphazardly harvesting mature Honeycrisp apples from the CU orchard in our experimental rows and measuring aborted seeds (median = 1.3, mean = 1.44).

Once functional relationships between pollen deposition and both fruit and seed set were modelled with GLMMs (see *Data analyses* section below), we translated per-visit pollen deposition by free-flying visits to per-visit fruit and seed set.

Importance. We derived a bee group's pollinator importance at each farm for 2011 and 2012, by the product of a bee group's relative abundance per year and predicted fruit set from NS, where we had data for all three bee groups, a blocked study design and higher sample size. Mean standard errors of importance were derived using the delta method (Powell 2007). We did not use predicted seed set in importance calculations because seed set was highly correlated with fruit set and the latter has more direct implications for production.

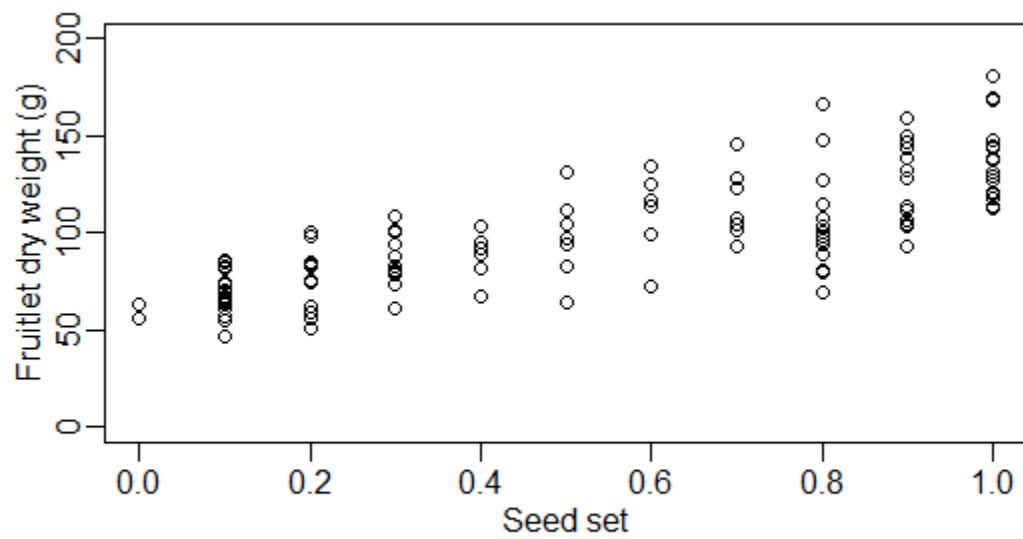


Figure 1.3. Relationship between seed set and fruitlet size at Nova Scotia orchard.

Data analyses. We used descriptive statistics to compare frequencies of natural foraging behavior observed among interviewed bees, in 2010 at CU. To test the fixed effects of visitor, visit duration, presence of pollen loads, foraging approach, reward sought and their interactions, on pollen deposition for free-flying bees, we used a generalized linear model (GLM) with a negative binomial distribution (Zuur et al. 2013). We excluded *Bombus* from the model given its small sample size ($n=8$). *Bombus*-included models kept presence of pollen load in, but removed visitor; while *Bombus*-excluded models kept visitor in but not pollen load. For the GLM, if the approach was mixed (top- and side-working), we reclassified it as topworking, and if foraging was mixed (pollen and nectar), we called it pollen foraging. All models were reduced using backwards step-wise selection to retain only those variables that had a significant effect ($p < 0.05$) and contributed to model fit. Starting with the interaction terms, we removed variables that were not significant ($p > 0.05$) and used a log-likelihood ratio test to compare the fit of the model with and without the term. If model fit did not change significantly ($p > 0.05$), then we kept the variable out (Zuur et al. 2013). Differences in mean pollen deposition were derived from this model.

Analyses on manual bee manipulations at CU and NS were conducted separately due to different experimental designs. For CU and NS, we ran normally distributed GLM and generalized linear mixed models (GLMM), respectively, to test the fixed effects of visitor and pollen load size on pollen deposition (ln-transformed) from hand-applied bees. For the NS GLMM, we added pollen source (thorax or scopa) as a fixed factor and tree as a random blocking variable. Both models were reduced with stepwise backward deletion as described above. To compare pollen deposition among hand-applied bee groups, we performed pairwise post-hoc Tukey's adjusted tests after each model. We similarly compared means of fruit set, seed set, and fruit weight (described below) at NS with post-hoc pairwise Tukey's adjusted tests.

To develop functional relationships between per-visit pollen deposition of the various visitors and fruit and seed set, we ran parallel models on the response variables fruit or seed set with pollen deposition (ln-transformed), visitor and their interaction as fixed factors. A significant interaction would indicate that the functional relationships vary among bees. We used a binomial GLM for the fruit set model at CU, but were unable to conduct a meaningful seed set model due to an inadequate sample size ($n = 13$). The NS model for fruit and seed set were similar to the CU model except, to account for dependence among clusters that received pollen from the thorax or scopa of the same bee, we included a random term consisting of the individual bees ID nested within tree. The fruit set and seed set models followed binomial and normal distributions, respectively. All models were reduced using backwards step-wise selection as described above. To further test effects of floral visitor, pollen deposition and their interactions on fruit quality, we conducted parallel, normally distributed GLM on fruit size, and a Poisson GLM on the number of carpels with developing seeds.

Due to non-normality of data, we used non-parametric Kruskal-Wallis to test differences in relative abundance, estimated fruit and seed set, and resulting pollinator importance among bee groups. Non-parametric pairwise Wilcoxon post-hoc tests were used to further explore differences between bee groups, with Bonferroni correction.

We verified that assumptions of normality and heteroscedasticity were met, and that Poisson and negative binomial models were not overdispersed. Analyses were conducted in R (R Core Team 2013). Normal and binomial GLMM models were conducted in ‘nlme’ (Pinheiro et al. 2014) and ‘lme4’ (Bates et al. 2011) packages in R, respectively, and their degrees of freedom were derived using Penalized Quasi-Likelihood in R package ‘MASS’ (Venables and Ripley 2002).

Results

Relative abundance. Study-wide, the relative abundance of bees varied significantly both years (2011: $\chi^2_2 = 25.63$, $p < 0.0001$; 2012: $\chi^2_2 = 44.6119$, $p < 0.001$) with relative abundance of *Apis* higher than that of *Bombus* and *Melandrena* both years (2011 and 2012, $p < 0.001$), and relative abundance of *Melandrena* higher than that of *Bombus* in 2012 ($p = 0.04$; Figure 1.4a). At the farm-level, relative abundances varied widely (Figure 1.4b).

Free-foraging pollination. During observations of natural foraging behavior among tree rows, *Apis* side-worked apple flowers disproportionately more than *Melandrena* and *Bombus* (see Table 1.2 for summary of all foraging data). Of all observed bees, about 90% *Melandrena* and 50% *Bombus* and *Apis* foraged for pollen. *Melandrena* were slower visitors than *Apis*, taking twice as long per flower, visiting fewer flowers/min and trees/min, and taking twice as long to disappear from the observer's sight. *Bombus* was the fastest visitor, taking half as much time as *Apis* at each flower. Approach behavior at emasculated flowers during interviews was similar to that observed in natural conditions; however, bees disproportionately foraged for nectar compared with pollen, and honey bees spent more than twice as long at interview flowers as *Melandrena*.

Per-visit pollen deposition varied among free-flying bee groups ($\chi^2_3 = 18.37$, $p < 0.001$). On average, *Melandrena* and *Bombus* deposited about 2.5 and 1.5 times more pollen, respectively, than *Apis* per-visit (Figure 1.5). Opportunistically sampled *Xylocopa virginica* deposited orders of magnitude more pollen than other bees (588.09 ± 188.92 , $n = 11$). Topworking and nectar-foraging bees deposited more pollen than sideworking and pollen-foraging bees (Table 1.3). After controlling for the influence

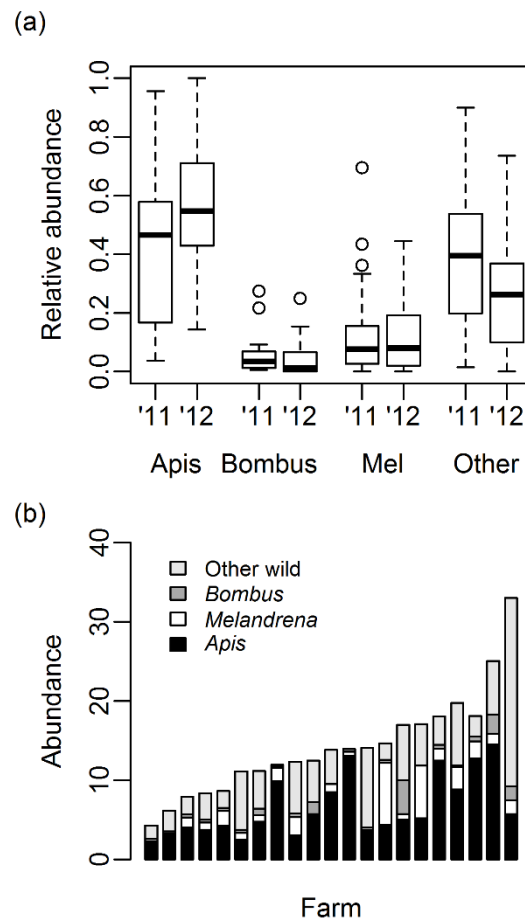


Figure 1.4. Relative abundance study-wide in 2011 and 2012 (a) and average abundance per transect per farm across years (b) of *Apis*, *Melandrena*, *Bombus*, and all other wild bees.

Table 1.2. Frequencies of foraging behaviors for free-flying *Apis*, *Melandrena*, and *Bombus* observed in 2010 and 2011 at Cornell University Orchards. Free-flying observations of *Xylocopa virginica* included. Data are %, means \pm SEM or medians (min – max).

	<i>Apis</i>	<i>Melandrena</i>	<i>Bombus</i>	<i>X. virginica</i>	Test (<i>p</i> -value)
Natural flowers 2010					
n	153	51	14	32	
Approach (%)					
Sidework	34.6	3.9	0	6.3	$\chi^2_6 = 42.17$
Topwork	60.1	88.2	100	90.6	(< 0.0001)
Mix	5.2	7.8	0	3.1	
Reward sought (%)					
Nectar	52.9	9.8	57.1	78.1	$\chi^2_6 = 63.02$
Pollen	42.5	60.8	21.4	12.5	(< 0.0001)
Both	4.6	29.4	21.4	9.4	
Visit length (sec)	4.4 (1.0 - 27.3)	8.2 (1.1 - 86.1)	2.1 (1.0 - 8.5)	2.1 (0.5 - 5.7)	$\chi^2_3 = 58.01$ (< 0.0001)
Natural flowers 2011					
Approach (%)					
Sidework	63.6	20.9			$\chi^2_1 = 16.85$
Topwork	36.4	78.1			(< 0.0001)
n	44	43			
Reward sought (%)					
Nectar	70.45	51.2			$\chi^2_2 = 3.98$
Pollen	16.0	32.6			(0.14)
Both	13.6	16.3			
n	44	43			
Time in sight (sec)	73.3 (9.9)	127.2 (21.7)			$t_{60} = 2.26$
n	46	44			(0.028)
Flowers /min	7.8 (0.5)	4.3 (0.32)			$t_{73} = -5.57$
n	46	44			(< 0.0001)
Trees/mins	2.20 (0.44)	1.55 (0.41)			$t_{60} = -1.08$
n	29	33			(0.28)
Interview flowers					
n	53	52	9	11	
Approach					
Sidework	53.2	17.1	0	0	$\chi^2_2 = 13.97$
Topwork	44.7	77.1	100	100	(0.0009)
Mix	2.1	5.7	0	0	
Reward sought					
Nectar	87.0	54.3	77.8	75	$\chi^2_2 = 11.0$
Pollen	2.2	40.0	22.2	12.5	(0.0042)
Mix	10.9	5.7	0	12.5	
Visit length (sec)	8 (0.5-48.72)	3.3 (0.39-39.8)	1.9 (1-5.9)	3 (0.5-7.5)	$\chi^2_3 = 13.27$ (0.0041)
Pollen load %					
Yes	26.9	92.3	75	63.6	$\chi^2_4 = 53.32$
No	73.1	7.7	25	36.4	(< 0.0001)

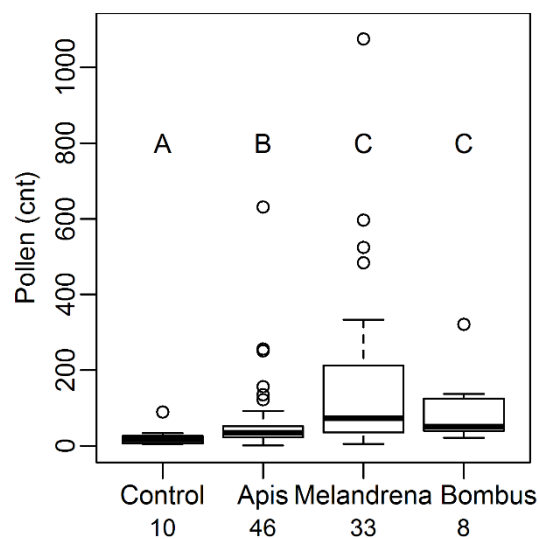


Figure 1.5. Differences in number of Rosaceae pollen grains deposited after a single visit on stigma of emasculated Honeycrisp flowers, by three bee groups studied: *Apis mellifera*, *Melandrena*, and *Bombus* spp. at the Cornell University study orchard. Pollen counts on negative controls also provided. Numbers below x-axis labels indicate sample size.

Table 1.3. Significant effects of foraging behaviors and pollinator identity on per-visit pollen deposition on apple flowers from bee interviews in 2010 at Cornell University orchards. Due to low sample size for *Bombus* ($n = 8$), only *Apis* ($n = 46$) and *Melandrena* ($n = 33$) were included. Approach refers to whether a bee side- or top-worked flowers and reward refers to whether bees collected pollen or nectar (mixed approach were considered a pollen visit for analyses). Non-significant interactions, visit duration, and presence of pollen load were excluded from final negative binomial model with $d.f. = 73$.

Effect	coeff. (\pm SE)	z-value	p-value	Significant differences
Pollinator	0.99 ± 0.26	3.854	0.00012	Mel > <i>Apis</i>
Approach	-0.78 ± 0.26	-2.97	0.0030	Top > Side
Reward	-0.87 ± 0.29	-3.045	0.0023	Nectar > Pollen

of flower handling and reward sought, some unmeasured characteristic(s) of *Melandrena* resulted in higher pollen deposition (significant pollinator effect; Table 1.3). Based on pollen deposition alone, native bees were more effective on a per-visit basis than honey bees.

Manual pollination. Pollen deposition resulting from hand-applied bees was more similar between *Melandrena* and *Apis* than that resulting from free-foraging visits and was positively associated with size of scopal pollen load. Pollen deposition was highest for *Melandrena*, intermediate for *Apis*, and lowest for *Bombus* at NS and higher for *Melandrena* than *Apis* at CU (Figure 1.6). While trends in pollen deposition mirrored those for free-flying bees, *Melandrena* and *Bombus* pollen transfer did not differ statistically from that of *Apis* (Table 1.4). Hand-applied *Bombus* left significantly fewer pollen grains than hand-applied *Melandrena* ($z = -2.68, p = 0.02$). At both sites, as size of scopal pollen load increased so did pollen transfer to stigmas (Table 1.4).

Both fruit yield (fruit set) and quality (seed set, fruit size, empty carpels) resulting from hand-applied bees were optimized by higher pollen loads on stigmas, regardless of bee or pollen placement. Consistently, fruit (Figure 1.7) and seed set (Figure 1.8) were highest for hand pollinated, lowest for negative control and intermediate for bee pollinated flowers. Relationships between probabilities of CU and NS fruit set and NS seed set and number of Rosaceae pollen deposited were significant (fruit set CU: $Z_{43} = 3.14, p < 0.01$; NS: $Z_{62} = 2.92, p < 0.01$; seed set NS: $t_{20} = 3.44, p < 0.01$) and followed a positive, saturating curve (Figure 1.9). The fixed effects of pollinator, pollinator \times pollen deposition, and pollen placement were not

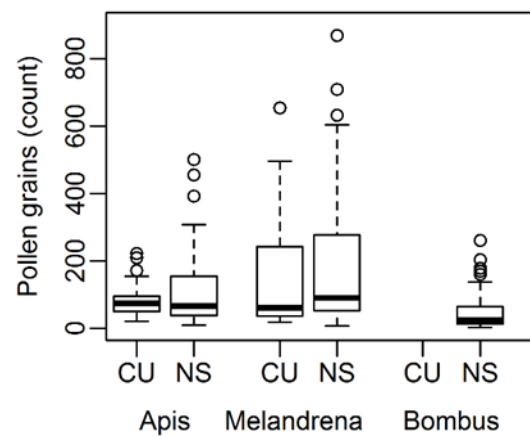


Figure 1.6. Pollen grains deposited from hand-applied *Apis*, *Melandrena* and *Bombus* at Cornell University Orchards, NY (CU) and at the Nova Scotia study orchard (NS).

Table 1.4. Significant effects of pollinator identity and pollen load size on (ln-transformed) per-visit pollen deposition resulting from hand-applied *Apis*, *Melandrena* and *Bombus* on apple flowers in 2011 at Cornell University (CU) and Nova Scotia (NS) orchards. At NS, tree was included as a random blocking factor. At NS, whether pollen came from the thorax or scopa was not significant and was excluded from final GLMM. Degrees of freedom for CU GLM was 39, for NS GLMM was 107. Coefficients are not back-transformed.

Effect	CU			NS		
	coeff. \pm SE	t-value	p-value	coeff. \pm SE	t-value	p-value
Pollinator (ref = <i>Apis</i>)						
<i>Melandrena</i>	0.011 \pm 0.21	0.045	0.96	0.34 \pm 0.20	1.66	0.10
<i>Bombus</i>				-0.27 \pm 0.23	-1.17	0.25
Pollen load size (ref = none)						
small	0.33 \pm 0.28	1.17	0.24	0.74 \pm 0.31	2.39	0.019
medium	0.90 \pm 0.30	2.99	0.0049	1.27 \pm 0.24	5.26	<0.0001
large	1.90 \pm 0.44	4.32	0.0010	1.56 \pm 0.26	5.83	<0.0001

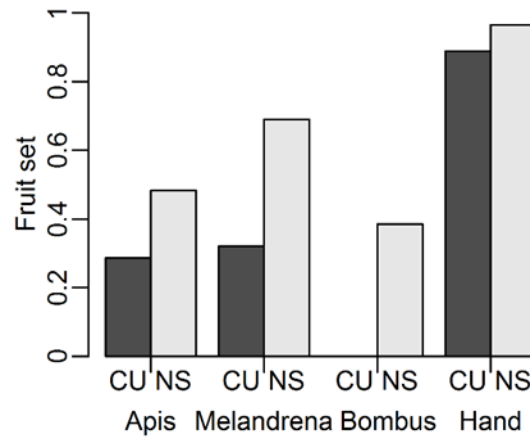


Figure 1.7. Rates of Honeycrisp fruit set after directly applying the underside of the thorax of immobilized bees and a positive control (“Hand” applied pure cross pollen) to the stigma, at Cornell University (CU) and Nova Scotia (NS) study orchards. Note: no *Bombus* treatment was applied at CU. Sample size for *Apis*, *Melandrena*, *Bombus* and Hand were as follows: CU = 28, 28, NA, 27; NS=29, 29, 26, 29.

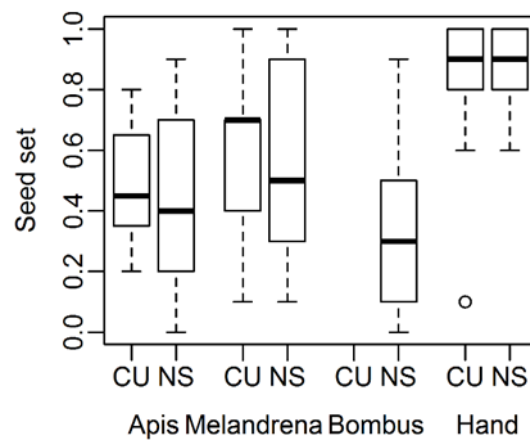


Figure 1.8. Proportion Honeycrisp seeds that set after directly applying the underside of the thorax of immobilized bees and a positive control (“Hand” applied pure cross pollen) to the stigma, at Cornell University (CU) and Nova Scotia (NS) study orchards. Note: no *Bombus* treatment was applied at CU. Sample size for *Apis*, *Melandrena*, *Bombus* and Hand were as follows: CU = 8, 24, 9, NA; NS = 14, 19, 10, 27.

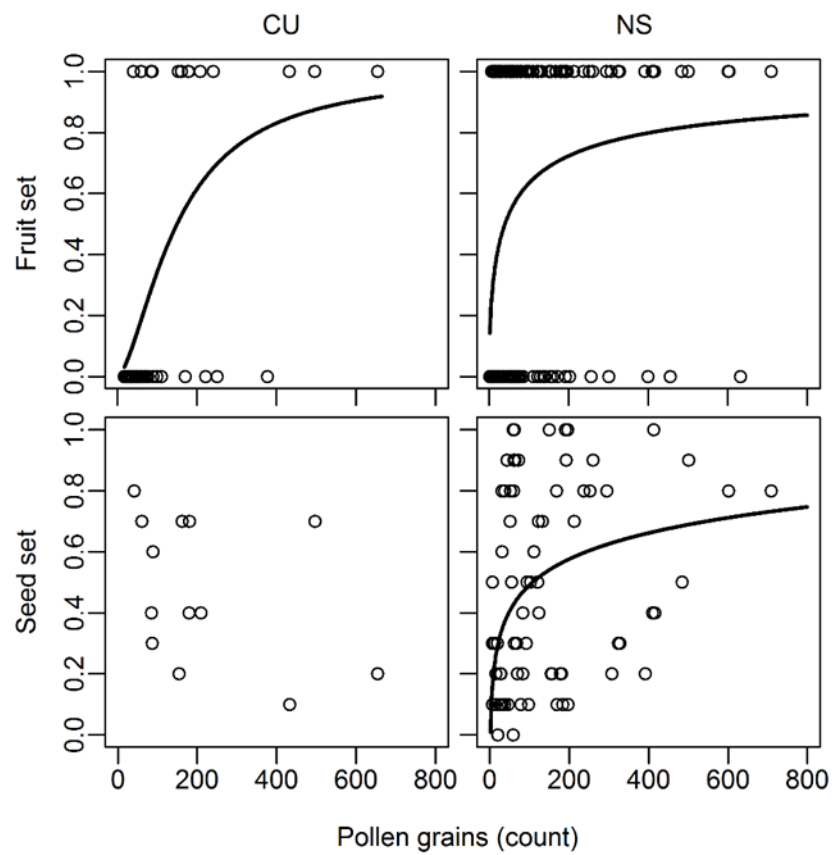


Figure 1.9. Relationships between Rosaceae pollen grains deposited from hand-applied bees and fruit set and seed set at Cornell University orchards (CU) and the Nova Scotia orchard (NS).

retained in the model, indicating 1) bees carried similar quality pollen and 2) pollen stored in the scopa was as viable as pollen from the thorax.

We observed a main effect of pollinator on fruit quality but not on yield. While flowers visited by the different bee groups were equally likely to set fruit, differences in seed set and fruit quality were observed, but only between *Melandrena* and *Bombus*, and mirrored differences in pollen transfer. Compared with *Bombus*, *Melandrena*-produced fruitlets had marginally higher seed set (*Bombus* v. *Melandrena*: 0.61 ± 0.058 v. 0.43 ± 0.081 [mean \pm SEM], $Z_{26} = -2.23$, $p = 0.07$; Figure 1.8) and were significantly larger (*Bombus* v. *Melandrena*: $4.33 \text{ g} \pm 0.059$ v. $4.56 \text{ g} \pm 0.048$; $t_{27} = 3.30$, $p < 0.01$). Fruit and seed set resulting from *Apis* visits did not differ significantly from those of *Bombus* or *Melandrena* ($t_{26} = 1.07$, $p = 0.29$; Figure 1.8). The more Rosaceae pollen transferred to stigmas, the fewer empty carpels were observed ($t_{77} = 2.20$, $p = 0.03$). Even though pollen deposition increased seed set, only seed set had a significant effect on fruit size ($t_{27} = 12.12441$, $p < 0.0001$, Figure 1.10).

Importance. Having translated pollinator effectiveness from per-visit pollen deposition by free-flying bees to per-visit fruit and seed set, we observed a smaller but significant difference in effectiveness among bee groups ($\chi^2_2 = 10.62$, $p = 0.005$), but only between *Melandrena* and *Apis* ($p = 0.007$, Figure 1.11). Consequently, calculated contributions of pollinators at the orchard level mirrored relative abundances within orchards, with significant differences among bees in both years (2011: $\chi^2_2 = 21.80$, $p < 0.0001$; 2012: $\chi^2_2 = 44.66$, $p < 0.0001$). Bees ranked from highest to lowest importance as follows: *Apis* > *Melandrena* > *Bombus* (Figure 1.12). *Apis* had significantly higher pollinator importance than *Melandrena* (2011: $p < 0.05$; 2012: $p < 0.0001$) and *Bombus* (2011 and 2012: $p < 0.0001$). *Melandrena* pollinator importance was

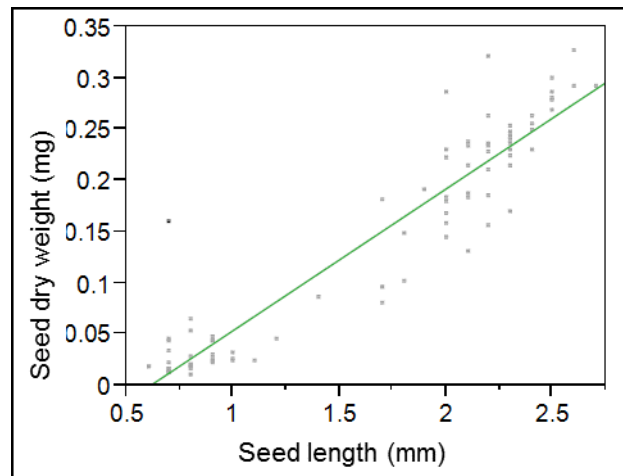


Figure 1.10. Correlation between seed length and mass from Nova Scotia fruitlets.

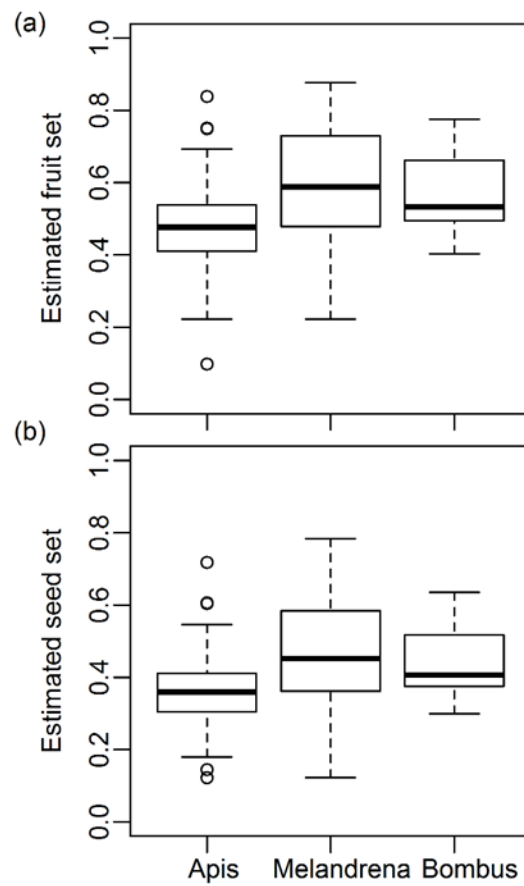


Figure 1.11. Estimated per-visit probabilities of fruit (a) and seed set (b) for *Apis*, *Melandrena* and *Bombus*, based on free-flying bee pollen deposition and relationships between pollen deposition and reproductive success at NS.

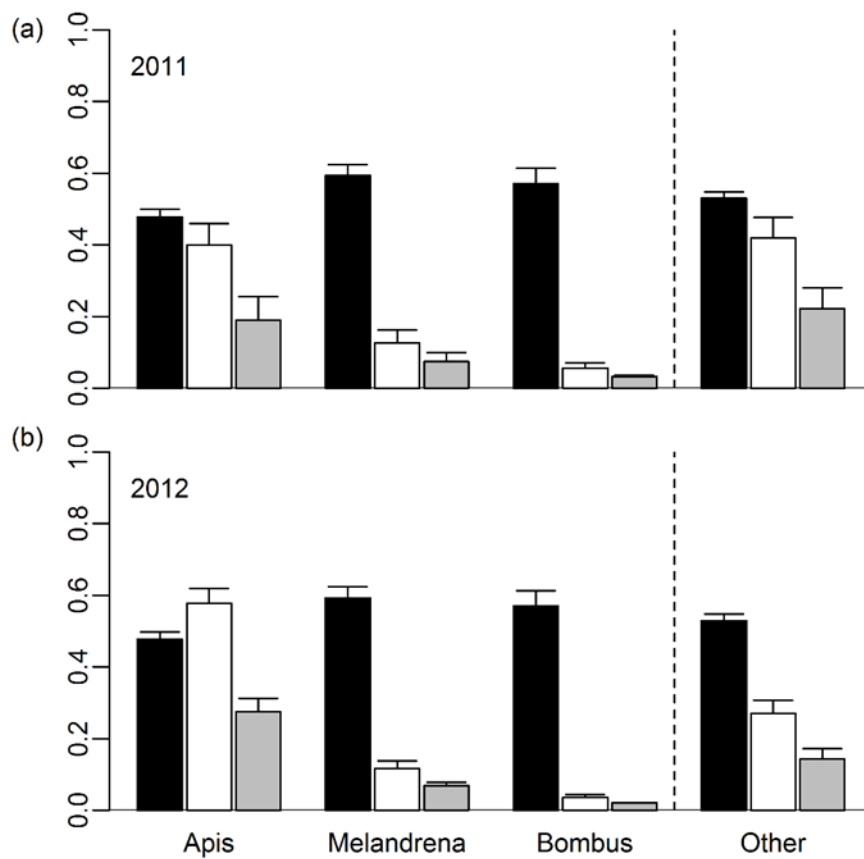


Figure 1.12. Predicted fruit set (black), relative pollinator abundance (white), and calculated pollinator importance (grey) of three focal bees visiting apple in 2011 (a) and 2012 (b). On right side of dotted line, projected pollinator importance of all other wild bees is provided, for estimated fruit set is the average predicted fruit set from the three focal bees: *Apis*, *Melandrena* and *Bombus*. Data are means + 1SE.

significantly higher than that of *Bombus* in 2012 ($p = 0.002$). While not included in the above analyses, pollinator importance of other wild bees, combined, was similar to that of *Apis* especially in 2011 (Figure 1.12).

Discussion

As honey bee declines make it more difficult for apple growers to rent honey bees for pollination, the question of whether growers can rely on wild bees becomes increasingly relevant. Per-visit, we found *Bombus* and *Melandrena* to be as effective pollinators as *Apis*. That apple yield and quality were optimized by higher pollen transfer, informs predictions about the quality of native bees not included in this study. While *Melandrena* and *Bombus* contributed more to pollination than *Apis* at two of our study farms, overall importance of *Melandrena* and *Bombus* was small within the study region. Given their functional equivalence, *Melandrena* and *Bombus* have the potential to compensate for honey bee losses, if orchards and their surroundings are managed to maximize their abundance. A more realistic and stable scenario for filling potential regional pollination gaps in orchards, however, is to focus on boosting entire communities of native bees, not just one or two species.

By translating pollen deposition to reproductive success, we provided a more refined comparison of per-visit effectiveness between two focal native bees and *Apis* for apple pollination (Cane and Schiffhauer 2003). Previous work identifying *Melandrena* and *Bombus* as potential alternative pollinators were based on pollen deposition and other proxies of pollinator efficiency: higher pollen transfer by *Bombus* compared with *Apis* (Thomson and Goodell 2001); high body counts and proportions of apple pollen found on *Bombus* and andrenids, notably *Melandrena* (Kendall and Solomon 1973, Boyle and Philogene 1983); and higher levels of *Bombus* and andrenid activity at lower temperatures (Boyle and Philogene 1983, Boyle-Makowski 1987).

Our study confirms that *Bombus* and andrenids, like *Melandrena*, are good pollinators of apple. Compared to *Apis*, *Bombus* and *Melandrena* transferred roughly 150 to 250 percent more pollen per visit. Because of a saturating relationship between pollen deposition and reproductive success (fruit and seed set), the highest rates of pollen transfer to stigmas by *Melandrena* and *Bombus* were superfluous. Consequently, effectiveness based on per-visit fruit and seed set estimates for *Melandrena* was about 20% higher than *Apis* and the effectiveness of *Bombus* was equivalent to that of *Apis*. Honey bees and *Melandrena* foraged within tree rows more than *Bombus* (pers. obs.); however, differences in movement did not measurably translate to higher pollen quality on their bodies, as evidenced by the lack of significant pollen deposition \times pollinator interaction terms in models where hand-applied fruit and seed set were the response variables. Though an improvement on pollen deposition alone, our assessment of per-visit pollinator quality still does not capture differences in visitation rates observed or documented differences in diurnal or temperature patterns of activity (Phillips 1933, Boyle and Philogene 1983).

Apple has previously been assumed to need but 10 viable pollen grains to achieve full fruit and seed set by pollination ecologists (Torchio 1983); however, regardless of pollinator, higher stigmatic loads of apple pollen significantly increased quantity (fruit set) and quality (seed set, carpel set and fruit size) of apple. Janse and Verhaegh (1993) previously showed this strong positive effect of pollen deposition on reproductive success, by systematically hand-applying a gradient of cross-pollen loads to apple stigmas. In addition, they determined a minimum threshold of 40 germinating pollen grains per stigma (or 200 apple pollen grains per flower) for optimal pollen-tube growth, which is close to where functional relationships between number of apple pollen grains and fruit and seed set began to saturate at NS (cool weather conditions at CU may have pushed the asymptote further). Mechanisms by which higher pollen

deposition could optimize reproductive success include 1) stigma priming, 2) reduced stigmatic clogging, and 3) increased distribution of pollen to stigmas. Larger pollen loads may insure adequate cross-pollen for fertilization, given a small proportion of the pollen may be needed to prime stigmas for pollen growth (Visser 1981, Janse and Verhaegh 1993). Independent of the pollinator, we observed a strong correlation between amount and proportion of apple pollen deposited on experimental flowers. Such a correlation would minimize stigma clogging by non-apple pollen, which has been shown to compromise fertilization of other plants (Shore and Barrett 1984). Higher pollen transfer may also increase likelihood that all five stigmas received adequate pollen for fertilization. Assuming Honeycrisp has imperfect syncarpy – which may not always be the case for apple cultivars (Sheffield et al. 2005) -- carpels are reproductively isolated and pollen transfer to all five stigmas would be necessary for maximal seed set and fruit quality (Free 1993). Because we mounted all five stigmas on each microslide for counting, we cannot discern whether each stigma received pollen, nor whether the distribution of fertilized carpels would have been affected. In sum, when assessing pollinator quality for apple, higher pollen transfer is desirable within the bounds of an upper threshold of roughly 200 grains per visit.

Our results validate the use of bee attributes that influence pollen transfer, specifically handling behavior, pollen counts on bodies and pollen placement, as proxies for apple pollinator effectiveness. As observed by Thomson and Goodell (2001), when bees topworked Honeycrisp flowers, stigma contact increased, resulting in higher pollen deposition. Sideworking, a form of nectar robbing, is a learned behavior used primarily by nectar-foraging *Apis*, which growers can manage by introducing naive colonies to orchards sequentially (Stern et al. 2007). Solitary native bees are less likely to sidework because they are primarily foraging for pollen and, therefore, have no reason to avoid anthers (Westerkamp 1991). Our observations that

pollen deposition increased with size of pollen load, supports the use of body pollen counts to identify, but not rank, quality pollinators for apple. Though corbicular pollen was as viable for fertilization as thoracic pollen, the likelihood of corbicular pollen contacting stigmas is low. It is likely that pollen loads indicate how much pollen is on the bodies in general and are not necessarily the source of pollen, per se. Body counts of pollen by Boyle and Philogene (1983) in Ontario, Canada, also found relatively high number of pollen grains on small *Andrena* and halictids, which make up the majority of other native bees visiting apple in New York and the Northeast. Generally pollen foragers have more pollen on their bodies and, therefore, transfer more pollen (Free 1993); however, nectar foraging resulted in higher pollen deposition in our study. We attribute this to the removal of anthers from experimental flowers, which altered pollen collecting behavior, or to the large quantity of nectar in virgin flowers that encouraged pollinators to probe flowers more deeply into the nectaries at the base of the flower (pers. obs). Finally, we speculate that dry storage of pollen in scopae near the abdomen and along the trochanteral and femoral scopa at the base of the hind legs of *Melandrena* contributed to significantly higher pollen transfer, after controlling for flower handling and reward. As in other megachilids, *Osmia* store dry pollen in scopaea scopa located on the underside of their abdomen and are excellent apple pollinators (Kuhn and Ambrose 1984, Vicens and Bosch 2000, Sheffield 2014). All *Andrena* species store pollen like *Melandrena*, suggesting that other andrenids would show similarly high quality as pollinators of apple flowers. Indeed, a sample of hand-applied, small andrenids, resulting in fruit set as high as our positive controls, supports high pollinator effectiveness among andrenids in general.

Together, *Melandrena* and *Bombus* provided a third of the pollination services that honey bees contributed to apple in central New York; however, their importance varied widely across farms and represents only a fraction of the entire native bee

community. The greater contribution of *Apis* across the region is, perhaps, not surprising given that we worked in a honey bee supplemented system. Honey bee supplementation could suppress *Bombus* visits to apple, if they compete for similar foraging resources (Heinrich 2004). Previous work observed more native bees visiting apple when honey bees were absent (Boyle-Makowski 1987), and two of our study farms-- both receiving adequate pollination -- had more *Melandrena* and *Bombus* where *Apis* was not abundant. Future honey bee declines in orchards may actually increase abundance and pollination services by native bees. *Melandrena* and *Bombus* are only 2 of 100 wild bee species that visit apple in northeastern USA. *Andrena*, *Bombus*, *Xylocopa virginica* and *Osmia* -- shown here or in previous studies to be good alternative pollinators (Vicens and Bosch 2000, Sheffield 2014) -- numerically comprise 90% of the native bee fauna, so most, if not all, of the native bee community is pollinating apple efficiently. Native bee abundance in New York State is high, with more than half of study orchards having as many wild bees as honey bees (Figure 1.4). If we consider the ability of the entire native bee community to compensate for honey bee losses, then we envision a much more optimistic outcome for the potential of native bees to fill pollination gaps left by honey bees (Figure 1.12).

As *Apis*, *Melandrena* and *Bombus* were similarly effective per-visit, the contribution of a particular pollinator to apple production across orchards and within the region depended on its abundance. Theoretical and empirical work in other systems support the central role numerical dominance plays in determining pollinator importance (Olsen 1996, Vázquez et al. 2005). The direct relationship between abundance and pollinator contribution facilitates the use of optimal honey bee densities in orchards to define desirable rates of native bee visitation for apple. Brittain (1933) did just this in Nova Scotia, by counting relative numbers of *Apis* and solitary bees visiting a standard number of blossoms per 10 minutes. Because he knew the

density of hives per orchard area, he developed orchard-specific counts per minute equivalent to 1 hive per acre, the recommended density at the time. In this way, average solitary bee abundance was found to equal roughly 1 hive of honey bees per acre, and the effective population size of native bees was deemed large enough to support apple production in the region. Using relative abundance per se, Boyle-Makowski (1987) found native bees, particularly *Andrena* and halictids, to be important during years of poor weather since honey bee visitation was low under these conditions. Optimal bee density will be context specific, varying with bloom density, spacing of pollinizers, as well as the amount of blooming apple surrounding the focal orchard as bee abundance may dilute across more blossoms (Brittain 1933). Development of protocols that monitor native bee abundance in a context-specific, reliable, and easy manner is central to providing growers with the information they need to assess native pollination services available to them.

Transitioning an orchard to rely more heavily on wild pollinators may require actions on the grower's part to increase native bee abundance. Growers may optimize native bee abundance by minimizing pesticide use, maximizing natural areas surrounding their farms, and creating additional habitat and foraging resources for bees near orchards (Watson et al. 2011, Park et al. in review). Alternatively, is it possible for the apple industry to safely shift their pollination paradigm from one that maximizes fruit set and then reduces set by chemical thinning to one that is tolerant of less fruit set? A new horticultural approach called "precision thinning" is being implemented in New York State to systematically achieve optimal fruit set based on carbohydrate and fruit growth models (Robinson et al. 2013). By giving growers a calculated method to achieve targeted fruit set for their crop, perhaps over time, growers will be able to comfortably aim for lower initial fruit set that could be provided by fewer honey bees or by wild pollinators alone.

Honey bees are important for apple production and for some orchards in the Northeast, surrounded by little natural habitat with aggressive pesticide regimes, are necessary to supply adequate pollination. However, native bees, such as *Melandrena* and *Bombus*, are as efficient pollinators as honey bees and are likely contributing more to apple pollination than growers realize. Managing orchards in a manner that supports abundant native bee populations will optimize the potential for native pollinators to fill future pollinator gaps left by declining honey bees and, at the same time, support healthier honey bee populations.

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CHAPTER 2

COMBINED EFFECT OF PESTICIDES AND LANDSCAPE SIMPLIFICATION COMPROMISES WILD POLLINATORS

Abstract

Wild bee communities provide underappreciated but critical pollination services for our most valuable and nutritious crops. Given predicted global shortages in pollination services from honey bees, managing agroecosystems in a manner that supports thriving wild bee communities is central to ensuring sustainable and affordable food production. Natural areas surrounding farms generally benefit wild bee communities, but effects of pest management on bees are not well understood and potential interactions with natural areas are unknown. Here, we assess the effect of conventional pesticide use within a gradient of landscape simplification on the wild bee community visiting apple (*Malus pumila* Mill). Wild bee community abundance and species richness exhibited a negative dose response to increasing intensity of pesticide use in orchards one year after application. A significant contribution of fungicides to observed pesticide effects suggests important deleterious effects of pesticides, until recently, considered benign to bees. The effect of pesticides on wild bees visiting apple depended significantly on the landscape context and was buffered by natural habitat in the surrounding landscape. We establish a strong negative association between pesticides and the visiting wild bee community and a capacity for surrounding natural areas to facilitate resilience to this on-farm disturbance. Our results extend our understanding of the benefits natural areas have for wild crop pollinators and highlight the importance of integrating habitat complexity when weighing the costs of pest management on crop pollination services. Specifically, high

habitat complexity near orchards facilitates pollination while low habitat complexity near orchards results in higher ancillary “costs” of pesticide use due to lost pollination services.

Introduction

Adequate crop pollination is required to sustain an ever-increasing human population. Today 35% of global food production, including our most nutrient-rich crops (Klein et al. 2007, Eilers et al. 2011), benefits from insect pollinators, primarily bees. As this proportion continues to increase through time (Aizen and Harder 2009) and pollinators experience marked global declines (Biesmeijer et al. 2006, Potts et al. 2010, Cameron et al. 2011, van der Zee et al. 2012, Burkle et al. 2013), experts warn of a “pollination crisis” (National Research Council 2007).

Although more than 20,000 bee species have been described (Ascher and Pickering 2013), pollination management in modern agriculture traditionally involves a single species, the European honey bee, *Apis mellifera* L., for pollination. However, steady declines in honey bee populations over the past 50 years (National Research Council 2007), and significant colony losses due to “Colony Collapse Disorder” (Oldroyd 2007, vanEngelsdorp et al. 2009), have resulted in costly hive rental fees and supply shortages for growers. Relying on a single pollinator species for food production is not only risky (Winfree 2008), it is inefficient. Globally, crop pollination consistently increases with wild bee but not honey bee abundance (Garibaldi et al. 2013). This suggests that wild bees may be able to compensate for continued honey bee losses, but honey bees cannot replace pollination services of wild bees (Tylianakis 2013). Abundance and diversity of bee communities drive pollination services, with abundance influencing the level of pollination received by the crop (Garibaldi et al. 2013), and diversity stabilizing pollination services through time and space (Kremen

et al. 2004, Klein 2009, Garibaldi et al. 2011). Pollination service resilience is particularly important in the face of rapid climate change (Bartomeus et al. 2011, Brittain et al. 2013). Strategies for sustainable food production must, therefore, include schemes to manage agricultural landscapes in a manner that supports both wild bee abundance and diversity (Garibaldi et al. 2013).

Agronomic practices have intensified dramatically within the last century, trading diverse small farms for large monocultures and increasing use of agrichemicals (Meehan et al. 2011). The risks to wild bees associated with habitat loss due to agricultural intensification are well-established (Kremen et al. 2007, Ricketts et al. 2008, Winfree et al. 2009, Viana et al. 2012, Kennedy et al. 2013). In contrast, we know little about how wild bee abundance and diversity respond to farm level pesticide exposure within agroecosystems. Mass die offs of wild bees inadvertently exposed to insecticides (Kevan 1975) demonstrate acute, lethal effects of pesticides at population and community levels. Individual lab and field toxicity tests on managed bees show that pesticides have sublethal effects on individuals with ramifications for bee populations and communities, as well (Desneux et al. 2007, Mommaerts et al. 2010, Henry et al. 2012, Whitehorn et al. 2012, Pettis et al. 2013). Individual toxicity tests have rarely been conducted on wild bees (but see Ladurner et al. 2005, Alston et al. 2007). Wild bee communities comprise a diverse assemblage of species varying in size, life history and foraging strategy, all of which influence exposure probability and susceptibility to pesticides (Desneux et al. 2007, Brittain and Potts 2011). With over 100 residues found in honey bees and hives (Mullin et al. 2010), the number of pesticides to which wild bees are likely exposed, as well as unknown possible synergistic effects, makes predicting the community response to pesticides based on individual lab tests untenable. Field comparisons of organic and conventional farms have been the first to reveal measurable effects of increasing pesticide use on wild bee

communities (Kennedy et al. 2013). But because organic farming represents only 1% of US and global agriculture (USDA NASS 2011), such categorical comparisons leave us with a large gap in documenting the range of effects within conventional spray regimes. Field level studies addressing the combined effect of pesticides across a continuum of realistic conventional exposure rates on bee communities are urgently needed.

Both habitat simplification and increased agrichemical use may negatively affect wild pollinators and their services, yet little is known about their potential interactions. Natural areas provide food and nesting resources for pollinator communities leading to increased crop pollination services (Kremen et al. 2004). While these services have been shown to diminish as farming practices intensify (Kennedy et al. 2013), no one has yet examined whether natural areas have the capacity to mitigate the effects of pesticides on wild pollinator communities. If natural areas provide a large enough pool of wild pollinators migrating to a crop field or provide refuge from pesticides, they could theoretically buffer effects of pesticides. Understanding whether the impact of pesticides depends on the landscape context would inform accurate predictions and decision-making regarding the management of our agricultural landscapes.

Here, we use natural gradients of both conventional pesticide use and percent natural areas within the surrounding landscape to investigate 1) the effect of pesticides on wild bees visiting apple, an economically important crop, and 2) dependence of pesticide effects on the landscape context.

Methods

Study sites and system. The study was carried out late April to mid-May 2011 and 2012 in western and central New York State, USA. The study region spans

roughly 5,000 km² and ranges from Newfield in the south (42.351524°, -76.564604°) to the southern shore of Lake Ontario (43.282155°, -77.121445°) in the north. Sites were spread across five counties: Cayuga, Ontario, Schuyler, Seneca, Tompkins, and Wayne counties. Annual rainfall is approximately 1,000 mm. Average temperatures range from 0 °C and 27.5 °C. The study landscape is heterogeneous, marked by fragmented deciduous woodlands and mixed agriculture, and included three study regions: southern Fingerlakes, northern Fingerlakes and southern Lake Ontario. Apple production intensifies as one moves north from the southern Fingerlakes to Lake Ontario, the primary apple producing region of New York State, which is the second largest producer of apple in the United States (USDA National Agricultural Statistics Service 2008). Study sites included Upick, experimental and commercial orchards, ranging in size from 0.4 to 162 ha.

Apple is a perennial, mass-flowering crop that requires cross-pollination by insects, primarily bees (1). The general practice for managing pollination in our study region is to rent honey bee hives, particularly for large orchards (pers. obs). In our study, 74% of farms rented honey bees, at average density 0.42 hives per acre but ranged from 0.16 to 1.14 hives per acre. Apple is visited by a diverse and abundant wild bee community (2); it is an attractive and accessible floral resource for wild pollinators due to its open flower morphology and production of substantial nectar and pollen rewards (3). Although farms in our study displayed a wide range of pesticide use, managing a successful crop requires a relatively intense spray regime compared to other crops (4). Fungicides are applied throughout the season, especially before and during bloom. Growers protect pollinators from insecticide sprays by not applying them during the bloom; however, their precautions are traditionally based on timing of hive placement in the orchard just before the bloom and removal at petal fall. Insecticides are commonly applied before bloom to kill aphid and mite eggs, and at

petal fall, the end of peak bloom when petals start to fall, to control lepidopteran pests. Conventional apple growers ubiquitously apply thinning sprays to reduce the fruit load of trees in order to maximize fruit size and prevent alternate bearing among years. Thinners, including Carbaryl an insecticidal compound that also stresses apple trees and plant growth regulators, are typically applied at petal fall after honey bee hives have been removed. Depending on the fruit load, up to 25% of blossoms may remain on trees when thinners are applied. Therefore, in spite of grower efforts to protect pollinators from pest management, if active in the orchard before or near the end of bloom, wild bees are exposed to fungicides, bactericides, insecticides and plant growth regulators.

Bee sampling. We surveyed abundance and species richness of bees visiting apple blossoms in a total of 19 orchards (16 in 2011 and 19 in 2012), varying in intensity of conventional pest management and amount of surrounding natural habitat (Figure 2.1). Minimum distance between sites was 1.9 km to ensure independence among farms. Bees visiting apple were net-collected along 15-minute, standardized transects one to two times during bloom. During each 15 minute transect, collectors walked a steady pace along 50 m of each side of two-adjacent tree rows, and netted all observed bees visiting apple blossoms. Surveys were conducted on days with temperature > 60°F between 10:00 and 15:30. In 2011 and 2012, temperature data was recorded for each transect from the nearest weather station and hand-held temperature meter, respectively. We required that there be enough sun to cast a shadow.

To inform transect placement based on distance from edge and bloom density, in 2011, we randomly placed three pairs of transects at two edges and at the center of the orchard, for a total of six transects. Transects were spaced at least 50 meters apart.

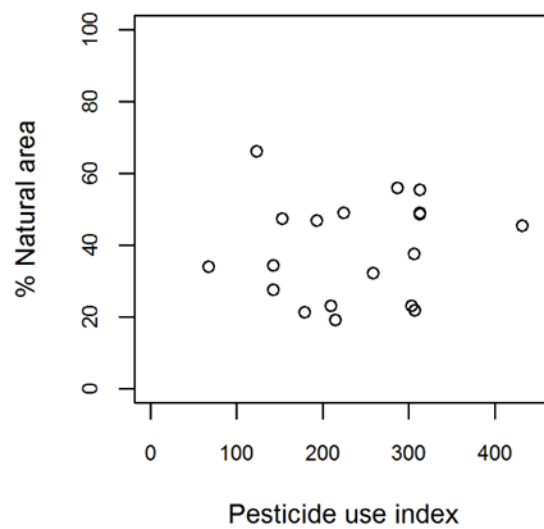


Figure 2.1. Study orchards (N = 19) lay along two continuous gradients: index of pesticide use intensity and landscape complexity (% natural areas), making it possible to look at the interaction between the two.

We conducted a minimum of two transects per collection event in our smallest orchards. If an orchard had a natural edge, we selectively placed a pair of transects there. The location of each transect was marked using GPS. We used ArcGIS 10 to map transects onto county orthophotos to calculate transect distance from orchard edge. In order to control for the effects of bloom display on bee visitation, we systematically counted the number of flower clusters (normally comprised of 5 flowers) and number of open flowers per cluster at the first, middle and last tree in a transect row. An estimate of the total number of blossoms per transect was then calculated by the product of number of trees per transect, average number of clusters per tree and percent open flowers. We also categorized the bloom stage at the orchard level as “early” (1-2 flowers open per cluster on average), “peak” (3-5 flowers open per cluster on average) or “past” (petal fall had begun), and the percentage of the orchard in bloom as 0-25%, 26-50%, 51-75% or 76-100%. The fixed effect of distance to edge, density of flowers in bloom per transect and their interaction were tested against wild bee abundance and richness per transect (both $\ln+1$ transformed) in a mixed linear model with the covariate temperature and farm as a random variable.

Because sampled bees were not influenced by distance from edge (abundance: $t = 0.92$, d.f. = 84, $p = 0.36$; richness: $t = 1.76$, d.f. = 84, $p = 0.082$) or bloom density within a transect (abundance: $t = -0.28$, d.f. = 84, $p = 0.78$; richness: $t = 0.17$, d.f. = 84, $p = 0.87$) in 2011, we simplified our sampling protocol the following year. First, we reduced number of transects per collecting event from six to two and placed them opportunistically throughout the orchard within 150 m of orchard edge, where trees were most in bloom. We maintained 50 m between transects whenever possible (if not, it was because bloom was limited or because orchard was too small). Second, we assessed bloom stage as described above, but did not count clusters per tree. Instead of calculating flowers per transect, we developed an index of bloom display for the farm

that incorporates the proportion flowers open per cluster within a transect and the proportion of the orchard in bloom. This index, therefore, estimated total floral display based on the bloom stage (relative to peak) of the trees and the spatial extent across the orchard. Given unequal sample sizes among farms within and between years, an average of timed netting trials was calculated per site per collection event and used in statistical analyses.

We also recorded density of honey bee hives at each site as they are commonly rented for pollination. Bee specimens were pinned, labeled and identified to species. Specimens reside in Cornell University's Entomology Collection (<http://cuic.entomology.cornell.edu/>).

Natural habitat. We used ArcGIS 10 (ESRI 2011) to quantify percent natural habitat surrounding each farm at various spatial scales from the Cropland Data Layer (CDL 2010; 30-m resolution), provided by U.S. Department of Agriculture National Agricultural Statistics Service (USDA NASS). Due to low accuracy of CDL to detect orchards, we merged the CDL with a hand-digitized layer of apple orchards created from USDA Agriculture Service Center (ASC) county-level, digital ortho-photos zoomed at 1:2000 (USDA ASC 2009; 1-m resolution). Land cover was consolidated from a set of over 100 predefined categories to 17 land cover classes, which were further consolidated into natural habitat, agriculture and developed land use. We quantified spatial extent of natural habitat within five GIS buffer radii (300 m, 500 m, 1000 m, 1500 m, and 2000 m) centered on study orchards. To inform the appropriate scale at which to use percent natural in our main analyses, we determined the scale at which percent natural in the landscape provided the best model fit (i.e. lowest AIC score). Five mixed linear models were conducted with the response variables abundance and richness of wild bee species, each, and included the fixed covariates percent natural area, year and temperature, with farm as a random variable. The radius

of percent natural area changed with each model and included 300m, 500m, 1000m, 1500m and 2000m. The scale that provided the model with the lowest AIC score was chosen (Table 2.1). We determined that 2 km was the scale at which percent natural area in the landscape provided the best model fit, and conducted all analyses with landscape data at this scale. Dominated by deciduous and mixed forest, percent natural habitat was negatively correlated ($t = -3.9203$, $df = 17$, $P = 0.001$, Pearson's product momentum) with percent land in agriculture, or agricultural landscape simplification.

Pesticide use intensity. Spray records from the entire 2011 growing season were collected from participating growers. To quantify spray intensity across farms, which use different compounds at varied rates and schedules, we modified the Environmental Impact Quotient (EIQ) Field Use Rating (Kovach et al. 1992), to develop an index of pesticide use intensity based on impacts to bees. The EIQ Field Use Rating has been found to be a reliable indicator of environmental impacts (Greitens and Day 2007). Each pesticide has an assigned EIQ value (last updated in 2010), a cumulative measure of predicted impacts to human, wildlife, beneficial insect, soil and water health (Kovach et al. 1992). Toxicity of a pesticide to honey bees falls under impacts to beneficial insects and is referred here as the bee impact quotient (BIQ). The BIQ is a product of a pesticide's scaled toxicity (1=low, 3=medium, 5=high) to honey bees (Morse 1984) and its residue time (Table 2.2 for study-wide list of pesticides used and BIQs). Each study site's pesticide use index was quantified by summing, across all pesticides used on apple within the orchard, the product of a pesticide's 1) BIQ, 2) percent active ingredient in material sprayed, and 3) application rate (quantity per acre, Equation 1) (Kovach et al. 1992). Our pesticide use index provides a per-acre calculation of the cumulative effect of a given farm's spray regime on bees; as such, it accounts for differences in farm size.

Table 2.1. AIC results for mixed-model regressions of wild bee abundance and species richness by percent natural habitat in the surrounding landscape, year and temperature. Bold indicates radius used for all analyses.

Wild bee	Radius (m)	AIC
Abundance	300	283.36
	500	281.64
	1000	277.60
	1500	276.95
	2000	275.76
Species richness	300	154.84
	500	153.18
	1000	149.10
	1500	148.20
	2000	146.12

Table 2.2. List of pesticides applied across study orchards. For study analyses, bactericides were classified as fungicides (F) and miticides as insecticides (I). Pesticide application frequency and rate ranges are for the entire study. All rates were converted to lb/ac or pt/ac for index calculations. The bee impact quotient (BIQ) is a relative impact score based on honey bee toxicity and residue time. Herbicides, adjuvants and penetrants were not included in index calculations and are not shown here.

Table 2.2

Mode of Action	Class	Active ingredient	Times applied	Min rate (lb or pt/ac)	Max rate (lb or pt/ac)	BIQ
Fungicide	F	<i>Bacillus subtilis</i>	8	2	2	3
Fungicide/Bactericide	F	Basic Copper Sulfate	13	2	6	9.3
Fungicide	F	Boscalid	2	0.1875	0.225	9.3
Fungicide/Miticide	F	Calcium Polysulfide	4	8	8	9.3
Fungicide	F	Captan	140	0.25	5	3
Fungicide/Bactericide	F	Copper Hydroxide	5	1.5	4	9.3
Fungicide	F	Cyprodinil	30	0.125	0.75	9.3
Fungicide	F	Difenoconazole	27	0.25	0.8	15
Fungicide	F	Dodine	2	2	2	9
Fungicide	F	Fenarimol	7	0.0375	0.75	3
Fungicide	F	Fenbuconazole	3	0.375	0.5	9.3
Fungicide	F	Kresoxim-methyl	12	0.09375	0.375	3
Fungicide	F	Mancozeb	85	0.5	6	9.3
Fungicide	F	Myclobutanil	21	0.0625	0.3125	9.3
Fungicide	F	Phosphorous Acid	6	1	1.75	3
Fungicide	F	Pyraclostrobin	2	0.1875	0.225	9.3
Fungicide	F	Pyrimethanil	3	0.4	0.6	3
Bactericide	F	Streptomycin sulfate	31	0.2	1.5	10.23
Fungicide	F	Sulfur	28	1.5	6	9.3
Fungicide	F	Tebuconazole	1	0.15625	0.15625	15
Fungicide	F	Thiophanate-Methyl	33	0.03125	5.6	9.3
Fungicide	F	Trifloxystrobin	27	0.025	2	9.3
Fungicide	F	Triflumizole	3	0.3125	0.3125	3
Fungicide	F	Ziram	1	1.875	1.875	3
Insecticide/Miticide	I	Abamectin	3	0.125	0.625	28.5

Table 2.2 (Continued)

Mode of Action	Class	Active ingredient	Times applied	Min rate (lb or pt/ac)	Max rate (lb or pt/ac)	BIQ
Miticide	I	Acequinocyl	1	0.875	0.875	3
Insecticide	I	Acetamiprid	47	0.15625	0.5	17.1
Insecticide	I	<i>Bacillus thuringiensis Kurstaki</i>	22	0.4	1.5	5.7
Insecticide	I	Beta-cyfluthrin	2	0.1	0.1	28.5
Insecticide/Miticide	I	Bifenazate	1	0.2	0.2	17.1
Insecticide	I	Carbaryl	26	0.09375	4	15
Insecticide	I	Chlorantraniliprole	10	0.15625	0.25	18.81
Insecticide	I	Chlorpyrifos	1	1	1	15
Insecticide	I	Emamectin Benzoate	2	0.15	0.3	15
Insecticide/Miticide	I	Fenpyroximate	9	0.09375	2	3
Insecticide	I	Imidacloprid	5	0.125	0.375	28.5
Insecticide	I	Indoxacarb	13	0.1	0.375	28.5
Insecticide	I	Lambda-Cyhalothrin	2	0.25	0.25	28.5
Insecticide	I	Methoxyfenozide	3	0.75	0.8	15
Insecticide	I	Phosmet	7	0.7	2.5	28.5
Insecticide/Miticide	I	Pyridaben	2	0.125	0.6625	28.5
Insecticide	I	Pyriproxyfen	2	0.3125	0.3125	3
Insecticide	I	Spinetoram	11	0.28125	0.40625	18.81
Insecticide	I	Spirotetramat	6	0.15	0.46875	5.7
Insecticide	I	Thiacloprid	16	0.05	0.5	9
Insecticide	I	Thiamethoxam	8	0.28125	0.3125	28.5
Insecticide/Fungicide	Excluded	Petroleum oil	2	5.12	8	18.81
Plant growth regulator	P	6-benzyladenine	2	1	1	3
Plant growth regulator	P	GA4, GA7	4	1	1.25	3

Equation 1. Pesticide use index = Σ (BIQ \times % active ingredient \times rate)

In addition to calculating an overall pesticide use index for the entire 2011 growing season, we examined whether compound class (i.e., fungicide vs. insecticide) and timing were important predictors of pesticide effects on bees. We subdivided overall spray data according to 1) three time periods: before, during and after apple bloom, and 2) three class categories: fungicide, insecticide, and plant growth regulators (PGR). Bactericides and acaricides were included in fungicide and insecticide categories, respectively. We conservatively defined bloom sprays to fall within a five week period around the bloom, starting one week before and ending four weeks after the first day of bloom. We derived first day of bloom from our observations of floral phenology during bee surveys and from consulting with growers. Our reasons for extending our definition of bloom a week on either end include: 1) bees have been observed to visit un-opened blossoms in the balloon stage, 2) bees visit old flowers that have lost their petals but still supply nectar, 3) late blossoms can be found weeks after peak bloom, and 4) our estimates of early bloom are accurate within 2-3 days.

BIQ values were unavailable for inert ingredients such as surfactants and adjuvants, in spite of recent demonstrated sublethal toxicity to bees (Ciarlo et al. 2012); nor were they available for fertilizers or several plant growth regulators (PGRs) used for thinning. We assumed that fertilizers are generally not toxic to bees and did not include them. Only one PGR, Prohexadione Calcium, used at our sites had an assigned BIQ, which was used for all other PGRs. Orchard use of petroleum and mineral oils applied early in the growing season resulted in disproportionately high pesticide use indices due to the large quantity of material used; we, therefore, excluded oils from index calculations.

Statistical analyses. To test the impacts of conventional pesticide use and landscape simplification on pollinating bee communities, we tested the fixed effects of surrounding land-use (% natural habitat at 2 km radius), index of pesticide use intensity, orchard bloom display, region, year and temperature in a general linear mixed model (GLMM) on wild bee species richness and abundance, as well as honey bee abundance (Zuur et al. 2013). We included density of honey bee hives in orchards in the honey bee abundance model. To investigate the dependence of the wild bee community response to pesticides on the amount of near-by natural habitat, we included an interaction term between percent natural area and the pesticide use index in all models. Percent natural area and pesticide use index were centered on the mean and temperature was log-transformed. We accounted for confounding effects between local complexity and pest management, by including a categorical covariate of farm complexity based on orchard size and crop diversity (Kennedy et al. 2013). Complex orchards included 1) orchards only growing apple and smaller than 10 ha, and 2) orchards growing additional fruit crops but smaller than 20 ha. All orchards with contiguous areas larger than 20 ha were categorized as locally simple. Orchard was included as a random factor to account for repeat visits within a sampling season. Because year had a highly significant effect on both bee richness ($t_{42} = -4.13$, $p < 0.001$) and abundance ($t_{42} = -4.38$, $p < 0.001$), we analyzed 2011 and 2012 separately. To test a potential lag response of bees to pesticide use, we ran parallel models that used the pesticide index from 2011 on bee abundance and species richness sampled in 2011 and in 2012. We used stepwise deletion to simplify models (where $p > 0.05$). Starting with interaction terms, the explanatory variable with the highest p -value was removed. We then tested loss of explanatory power resulting from variable removal, by comparing models with and without the variable using analysis of variance (maximum likelihood fitting). If models did not differ significantly ($p < 0.05$), the explanatory variable was

removed. We used maximum likelihood estimation during the deletion process, but fit final models using restricted maximum likelihood to provide unbiased model results (Zuur 2009). For estimates of model fit, we provide the between and within group variation explained by our final models compared to random intercept (or null) models, as well as the change in AIC. We ran analyses on wild social and solitary bees separately in order to determine whether social behavior altered the response to pesticide use.

In order to differentiate pesticide effects due to insecticides and fungicides and the timing of their application, pesticide use indices attributed to each chemical class within each of the three time periods (before, during or after bloom) were recalculated per farm. Visual assessment of insecticide use after bloom revealed a disproportionate contribution of the insecticide Phosmet to the index, causing three farms to be outliers. We, therefore, recalculated insecticide indices for all farms across all time periods without Phosmet. Where final GLMM models for total wild bee abundance and richness included a significant effect of pesticide use index (2012), we reran final models with fungicide and insecticide use indices treated separately in place of the original combined pesticide use index, including new interaction terms with percent natural area. We also included a categorical Phosmet factor to test whether we missed an important influence of bee communities by excluding this compound. The effects of fungicide and insecticide use indices were compared within a single time period, resulting in three parallel models for each bee response variable. We proceeded with stepwise deletion as described above. For all models, the fixed effect of Phosmet was not significant.

Wild and solitary bee response variables were $\ln(y+1)$ transformed and a normal distribution was used. We verified data met assumptions of normality and homoscedasticity. Because transforming social bee responses did not meet these

assumptions, we rounded the data and used a Poisson distribution. We analyzed data with and without male bees and found that excluding males improved model fit but did not change overall results. We, therefore, present analyses without males. Sample independence was verified by visually assessing GLMM residuals for spatial autocorrelation, using sample variograms (Fortin and Dale 2005). All statistical analyses were conducted using R [41], including GLMMs using the “nlme” and “lme4” packages.

Results

Apple-visiting bee communities. In 2011 and 2012, we conducted a total of 320 standardized transects across 16 and 19 orchards, respectively, for 80 hours of active net-collecting of bees visiting open apple blossoms. We collected a total of 2990 wild bees, comprising 82 species, and 2569 honey bees. The wild bee community was numerically and taxonomically dominated by solitary, ground-nesting *Andrena*, commonly known as mining bees (2196 individuals, 27 species). Eight *Bombus* species made up less than 8% of wild bees collected and were primarily early spring foundress gynes (new queens), with *B. impatiens* Cresson comprising 70% of bumble bee individuals collected.

Effects of landscape context and farm pesticide use. Honey bee abundance was driven by temperature alone ($t_{46} = 2.43$, $p = 0.02$; Table 2.3 for full statistics), while wild bee communities were driven by temperature, characteristics of the landscape and farm management. Wild bee abundance and species richness increased with percent natural area in the surrounding landscape in both years (2011 and 2012 abundance, respectively: $t_{14} = 3.00$, $p < 0.01$ and $t_{15} = 4.29$, $p < 0.001$; 2011 and 2012 richness: $t_{14} = 2.79$, $p = 0.01$ and $t_{15} = 5.16$, $p < 0.001$, Table 2.3 for full statistics; Figure 2.2), and

Table 2.3. Fixed effects of pest management, percent natural habitat and environmental variables on abundance and species richness of wild bees visiting apple blossoms in 2011 and 2012, with a random orchard effect. All response variables were $\ln(y + 1)$ transformed and temperature was $\ln(x)$ transformed. Percent natural habitat and Pesticide Use Index (PUI) were mean centered. Non-transformed coefficients (SE) are presented with p -values indicated by asterisks: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Blanks represent variables dropped following backwards stepwise deletion.

Hive density had no measurable association with honey bee abundance, nor did complexity or floral display with bees overall and are not included. Orchard N=16 in 2011 and N=19 in 2012.

Table 2.3

Fixed Effects	Abundance							Species richness					
	Wild bee		Solitary		Social		Honey bee	Wild bee		Solitary		Social	
	2011	2012	2011	2012	2011	2012	^a	2011	2012	2011	2012	2011	2012
% Natural	0.038 (0.012) **	0.028 (0.0066) ***	0.033 (0.014) *	0.024 (0.0070) **	0.0976 (0.027) ***	0.069 (0.017) ***		0.023 (0.0083) *	0.025 (0.0048) ***	0.020 (0.0081) *	0.025 (0.0045) ***	0.071 (0.030) *	0.057 (0.018) ***
Pesticide Use Index (PUI)		-0.0036 (0.0010) **		-0.0034 (0.0011) **					-0.0027 (0.00073) **		-0.0026 (0.00069) **		
% Natural x PUI		0.00028 (8.6x10 ⁻⁵) **		0.00034 (9.0x10 ⁻⁵) **					0.00020 (6.2x10 ⁻⁵) **		0.00024 (5.9x10 ⁻⁵) ***		
Temp (C°)	1.81 (0.68)*	1.12 (0.46)*	2.00 (0.81)*	1.19 (0.47)**			1.00 (0.41)*	1.64 (.51)*	0.91 (0.34)*	1.62 (0.57)*	1.01 (0.32)**		
Region (0=Geneva) Lake Ontario					-2.34 (0.95)*							-01.88 (0.97)	
South Finger Lakes					-0.51 (0.80)							-0.62 (0.84)	
% Variation explained:													
Between	8.3	100	0	90.9	100	100	0	0	100	100	0	100	100
Within	51.0	31.2	44.6	22.6	100	100	12.3	55.3	36.7	36.1	43.3	100	100

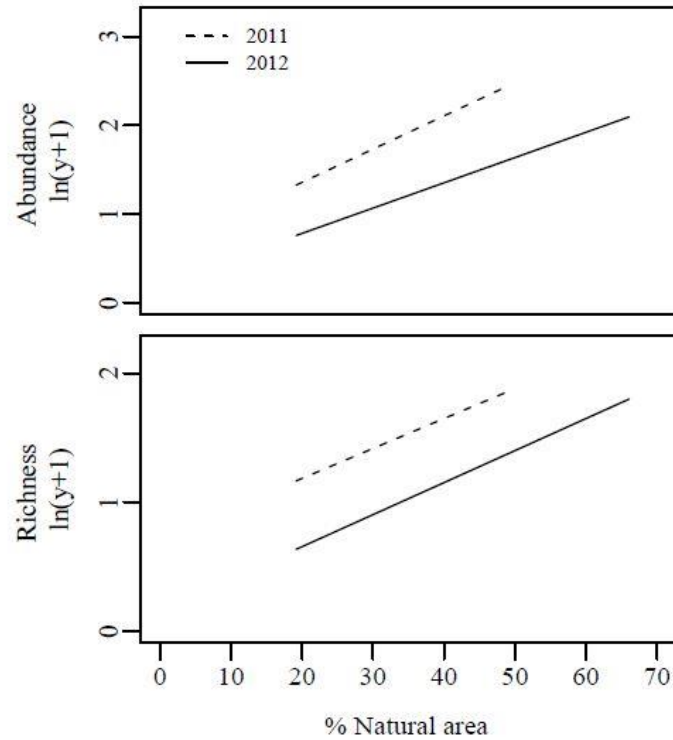


Figure 2.2. Bivariate relationships between surrounding natural habitat (2km scale) and average wild bee abundance and species richness per transect in apple orchards in 2011 (open circles; $N = 16$) and 2012 (closed circles; $N = 19$). Percent natural area had a significant positive effect on wild bee abundance (2011: $p = 0.008$; 2012: $p < 0.001$) and species richness (2011: $p = 0.01$; 2012: $p < 0.001$) across years. Data are fitted values derived from final GLMMs, with temperature held constant at 21°C , and span the observed range of natural area for the given years.

decreased in a linear fashion with intensified pesticide use one year after application (2012 abundance: $t_{15} = -3.53$, $p = 0.003$; 2012 richness: $t_{15} = -3.71$, $p = 0.0021$; Table 2.3 for full statistics; Figure 2.3a,e). Both social (2011 and 2012 abundance, respectively: $z_{12} = 3.37$, $p < 0.001$; 2012: $z_{17} = 3.98$, $p < 0.001$; 2011 and 2012 richness: $z_{12} = 2.39$, $p = 0.02$; $z_{17} = 3.19$, $p < 0.01$) and solitary bees (2011 and 2012 abundance: $t_{14} = 2.45$, $p = 0.03$; $t_{15} = 3.44$, $p < 0.001$; 2011 and 2012 richness: $t_{14} = 2.43$, $p = 0.03$; $t_{15} = 4.51$, $p < 0.001$) benefited from natural areas (Table 2.3 for full statistics, Figure 2.4). While having no measurable effect on social bees, increased pesticide use was associated with decreased solitary bee abundance (2012: $t_{15} = -3.22$, $p < 0.01$) and species richness (2012: $t_{15} = -3.73$, $p < 0.01$; Table 2.3 for full statistics, Figure 2.5). Overall pesticide effects on wild bees in 2012 were driven by fungicides applied early in the season (abundance, pre-bloom: $t_{15} = -2.99$, $p < 0.01$, Figure 2.3b; richness, pre-bloom & bloom: $t_{15} = -2.92$, $p = 0.01$ & $t_{15} = -2.32$, $p = 0.03$, Figure 2.3f,g) and insecticides applied after bloom (abundance: $t_{15} = -4.46$, $p < 0.001$; richness: $t_{15} = -4.85$, $p < 0.001$, Table 2.4 for full statistics; Figure 2.3d,h).

Susceptibility of wild bee communities to pesticides in 2012 depended on the amount of natural area in the surrounding landscape (significant percent natural \times pesticide use index interactions, Table 2.3; Figure 2.6). As natural areas within the surrounding landscape increased, the negative relationship between pesticides and wild bee abundance and species richness weakened.

Discussion

Global expansion of intensified agricultural practices threatens wild pollination, notably through habitat loss and increased use of conventional agrichemicals (Kremen et al. 2002, Klein et al. 2007). Agroecosystems that balance benefits of pest management with costs incurred to wild pollination services are

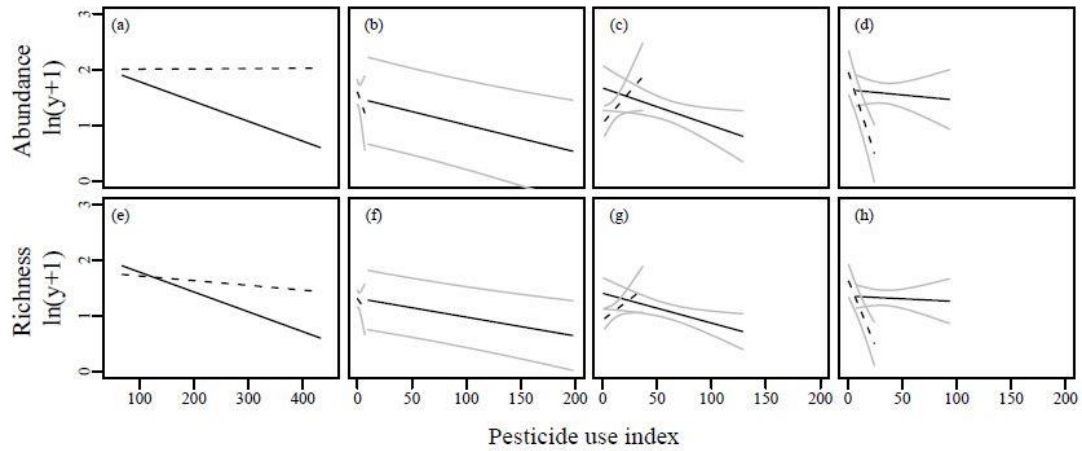


Figure 2.3. Bivariate relationships between intensity of conventional pesticide use in 2011 and average wild bee abundance (a) and species richness (b) per transect in apple orchards in 2011 (dashed line) and 2012 (solid line). Pesticide use had a significant negative effect on 2012, but not 2011, wild bee abundance ($p < 0.001$) and species richness ($p = 0.002$). For 2012, pesticide use indices are further separated by insecticides (dashed line) and fungicides (solid line) and three time periods: before (b,f), during (c,g) and after (d,h) bloom. Grey lines represent 95% CIs. Data are fitted values derived from final GLMMs with main effects of overall pesticide use, insecticide and fungicide use intensity included for visual representation if removed from final models, and temperature held constant at 21°C . Fungicides applied before bloom had a significant effect on 2012 wild bee abundance ($p = 0.009$) and species richness ($p = 0.01$). Species richness also had a significant negative relationship with fungicides applied during bloom ($p = 0.03$). Insecticides applied after bloom had strong negative associations with wild bee abundance ($p < 0.001$) and richness ($p < 0.001$).

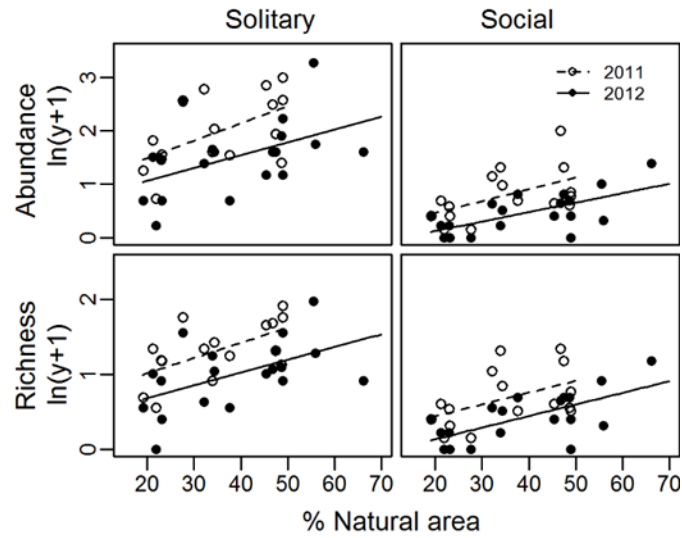


Figure 2.4. Bivariate relationships between surrounding natural habitat (2km scale) of wild solitary and social bee abundance and species richness in apple orchards in 2011 ($n=16$; open circles; hatched regression line) and 2012 ($n=19$, closed circles; solid regression line). Percent natural area had a significant positive association with all bee regardless of sociality across years ($p < 0.05$, Table S2). Simple linear regression lines indicate significant relationships.

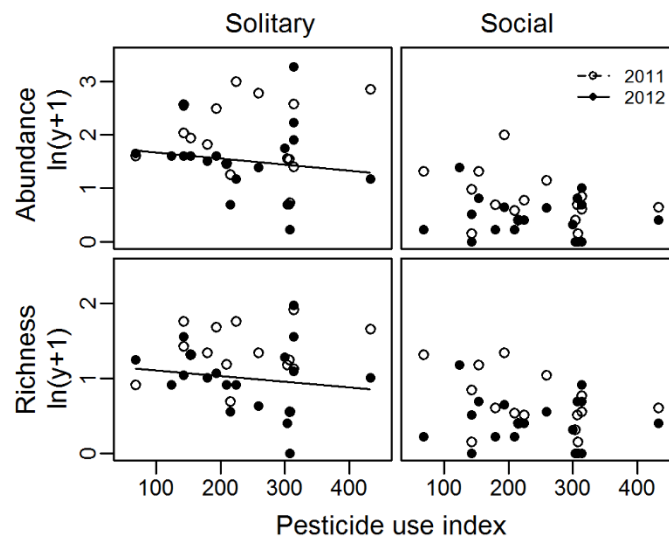


Figure 2.5. Bivariate relationships between intensity of conventional pesticide use and surveyed wild solitary and social bee abundance and species richness in apple orchards in 2011 (open circles, hatched regression line, $n = 16$) and 2012 (closed circle, solid regression line, $n = 19$). Pesticide use in 2011 had a significant negative effect on wild solitary bees (abundance: $p < 0.01$; richness: $p < 0.01$, Table S2) in 2012 but not in 2011. Simple linear regression lines indicate significant relationships.

Table 2.4. Effects of pesticides, according to class (fungicide v. insecticide) and timing of applications (before, during or after bloom), on wild bee abundance and species richness (per transect), surveyed on blossoms in apple orchards in 2012. Response variables were $\ln(y+1)$ transformed. All fixed effects were mean centered except for temperature, which was $\ln(x)$ transformed. Non-transformed coefficients (SE) are presented with p -values indicated by asterisks: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Blanks represent variables dropped following backwards stepwise deletion. There were no significant effects of Phosmet or insecticide x natural area interactions on bees and are not included. Orchard N=19 in 2012.

Fixed effect	Bloom		
	Before	During	After
Abundance			
Natural Habitat (%)	0.0080 (0.0065)	0.021(0.0087) *	
Fungicide Use Index (FUI)	-0.0044 (0.0015) **		
Insecticide Use Index (IUI)			-0.062 (0.0011) ***
% Natural x FUI	0.00032(0.00010) **		
Temperature	1.34 (0.46)	1.39 (0.49) *	1.73(.44) **
Species richness			
Natural Habitat (%)	0.0099 (0.0052)	0.021(0.0052) **	
FUI	-0.0032 (0.0011) *	-0.0056 (0.0011) *	
IUI			-0.047 (0.0097) ***
% Natural x FUI	0.00023(0.000076) **		
Temperature	1.07 (0.34) **	1.05 (0.36) **	1.45(0.34) ***

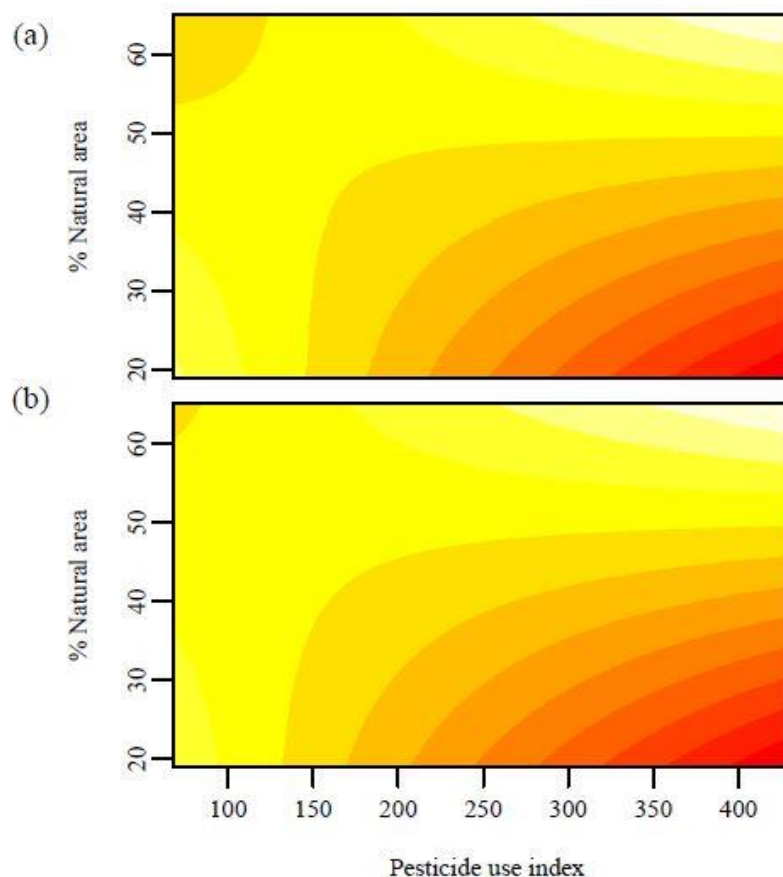


Figure 2.6. Heat maps of interactions between natural habitat surrounding orchards (% natural area at 2km radius) and intensity of conventional pesticide use (pesticide use index) in 2011 on wild bee abundance (a) and species richness (b) in 2012. As percent natural areas surrounding orchards increased, the negative relationship between increasing pesticide use and wild bees weakened. Data are fitted values derived from final GLMMs, with temperature held constant at 21⁰ C. Light yellow indicates highest and deep red indicates lowest wild bee abundance and species richness. Axes represent ranges of percent natural habitat and pesticide use index observed in the study.

needed (Deguines et al. 2014), but their design is hampered by our limited understanding of how agrichemicals affect wild bee communities in crop fields in varying landscape contexts. Here, we provide novel correlative evidence that abundance and diversity of wild bee communities in orchards are susceptible to increasing pesticide use, a risk that is buffered by natural habitat.

Surrounding natural areas acted as a source for wild bee pollinators of apple in upstate New York. Similar results were found for apple in Wisconsin (Watson et al. 2011) and other crop systems (Kevan 1975), where greater amounts of natural area in the landscape – or greater landscape complexity – led to a more abundant and diverse bee community. Extensive natural areas provide better nesting and foraging opportunities that allow for greater population sizes and species richness (Tschamntke et al. 2012). As bees are highly mobile organisms (Kremen et al. 2004) and apple is an attractive mass resource, community abundance and richness of wild bees in orchards were influenced by the regional landscape (a 2 km scale) and not necessarily the habitat immediately adjacent to the orchards. Since bees are central place foragers, larger spatial scales are not relevant over small time-periods.

Our approach of using an index to capture additive toxicity of pesticide programs across farms in a standardized manner is a flexible and effective method of characterizing spray intensity. While ours is the first to look at the combined effects of all pesticides applied, investigation of insecticide impacts on wild pollinators of Michigan blueberry with a similar index also found a linear, negative response of the bee community that was strongest the following year (Tuell and Isaacs 2010). Field studies focused on a single or select toxic insecticide(s) might miss important effects from heavily used pesticides considered to have low toxicity, like fungicides, or from synergies among compounds (Pilling and Jepson 1993, Sanchez-Bayo and Goka 2014). Such continuous and additive effects of pesticides are not measurable in

categorical comparisons (e.g., organic v. conventional), although these types of studies were the first to demonstrate a response of wild pollinators to varying intensities of pest management (Kennedy et al. 2013). A limitation of our pesticide use index, and of the EIQ field use rating from which it was modeled, is that index scores can be skewed by large rates of application, which is common practice for organic pesticide control products such as mineral oil. Therefore, we do not recommend using this index to compare conventional and organic farms, because organic pesticide regimes may receive inflated scores due to the sheer quantity of materials applied (Dushoff et al. 1994). The pesticide use index enabled us to combine continuous gradients of both conventional pesticide use and land use intensity to look at the landscape context of pesticide effects on bees.

By considering the full complement of pesticides applied in the field, our results show that intensified use of not only insecticides but also fungicides can render orchards a risky environment for wild pollinators. Similar to previous work focused solely on effects of insecticide applications on wild bees in in grape (Brittain et al. 2010) and blueberry (Tuell and Isaacs 2010), we observed a negative association between wild bee communities and intensified use of insecticides later in the season, attributed to additive sublethal exposure throughout the growing season. High exposure is the most likely explanation for why fungicides, with low honey bee toxicity (Johansen et al. 1983, Mayer and Lunden 1986), had a measurable impact on wild bees. Fungicides were most heavily employed in early spring when precipitation events were most frequent. During bloom, growers limit their use of insecticides to protect pollinators, but because fungicides are not labeled to protect bees, they are applied throughout the apple bloom and not uncommonly during peak hours of bee activity. Orchards with increased fungicide use during bloom had lower bee species richness. Because apple provides an attractive mass bloom and concentrates bees from

the surrounding landscape, spraying harmful chemicals during bloom could maximize likelihood of exposure. Significant effects of pesticide use throughout the growing season highlight the importance of minimizing pesticide use beyond the bloom period. Unlike honey bees that reside in orchards for the bloom period only, wild bees have a greater exposure risk to pesticides as they actively forage on flower resources located in and around orchards weeks before and after apple bloom (Bartomeus et al. 2013).

While we provide strong correlative evidence for an impact of fungicides on wild crop pollinators, the mode of action remains unclear. The lag in wild solitary bee response to increasing fungicide levels indicates reduced bee fitness. Altered foraging efficiency or nest recognition could decrease offspring production, but so could increased susceptibility of larvae to pesticides if toxins made it into pollen provisions. Honey bee pollen collected from orchards sprayed with fungicides had fewer beneficial fungal species (Yoder et al. 2013), indicating that digestion of pollen masses by larvae may be altered by fungicide exposure if such mutualisms are important for non-*Apis* nutrition, as well. In contrast to solitary bees, social bees did not respond measurably to pesticide applications in orchards. Divergent responses and sensitivities to pesticides of solitary and social bees are influenced by differences in life history traits, including number of generations produced within a season, foraging distance, diet breadth and when reproductives are produced (Brittain and Potts 2011). Given most lab toxicity tests are conducted on eusocial *Apis* and *Bombus*, the ability to accurately predict pesticide risk from lab toxicity tests for the whole pollinator community would benefit from the inclusion of non-*Apis* species (Fischer and Moriarty 2014). That fungicides are acutely and chronically toxic to solitary mason bees (*Osmia lignaria* Say) (Ladurner et al. 2005) also supports species-specific toxic thresholds among bees. Fungicides alone may have low toxicity, but they may interact with other pesticides or the inactive ingredients often included in spray formulations to

produce synergistically toxic effects (Pilling and Jepson 1993, Sanchez-Bayo and Goka 2014). Inactive ingredients, alone, can have lethal and sublethal effects on honey bees (Mullin et al. 2010, Ciarlo et al. 2012). While we may not fully understand the mechanisms, this study is the first to document a whole community response of wild bees to fungicide use at the farmscale, a finding that calls for further investigation into sublethal toxicity of fungicides on bees and for greater caution when using this class of pesticides when pollinators are actively foraging in or near crops.

That natural areas not only provide nesting and foraging resources but also dampen the effect of pesticides on the wild crop pollinators extends the benefits natural habitats have for wild bees and their services. Given the high mobility of bees, the capacity of natural areas to buffer the negative effects of pesticides on wild bees could be attributed to 1) greater provision of resources and 2) refuge from pesticides. Natural areas support crop pollinators, by providing vital foraging and nesting resources for population establishment and growth that are not available in agricultural fields. Deciduous or mixed forests were the major natural landcover in our study. Before canopies have closed, these forests are important for early spring pollinators (Watson et al. 2011). The more abundant and diverse the natural resources in a landscape, the larger, more diverse (Tscharntke et al. 2012), and possibly more healthy (Di Pasquale et al. 2013) the regional pool of bees are migrating to orchards.

Refuge from pesticide exposure, provided by natural areas in the agricultural matrix, could foreseeably insure health and survival of wild bee populations just as refugia in GMO-plantings prevents resistance in pest populations (Chaplin-Kramer et al. 2011). Conversely, bees foraging in landscapes dominated by agricultural areas where pesticides are applied, will have higher exposure risk even for pollinators surveyed in orchards with low pesticide use intensity (Yoder et al. 2013). Interactions between pesticide regime and landscape have been observed previously in studies

comparing bee diversity in organic versus conventional fields, with benefits of organic farming detected only in simplified landscapes (Holzschuh et al. 2007, Carvalheiro et al. 2010, 2012). Authors have generally attributed this pattern to higher floral resources typical in weedy organic fields within landscapes that offer few other floral resources. While this may indeed be the case, the inability of intensified landscapes to buffer conventional pesticides could also contribute to such patterns. Though pesticides depress wild bee communities, apple's mass bloom may provide important foraging resources that could boost bee populations (Westphal et al. 2003). An interesting direction for future study would be to identify a threshold of pesticide use given different levels of surrounding habitat, under which orchards could have a net positive effect on bee populations due to this mass bloom.

Evidence is building for the susceptibility of wild bee communities to pesticides in agricultural fields and landscapes (Holzschuh et al. 2007, Brittain et al. 2010, Tuell and Isaacs 2010, Carvalheiro et al. 2012, Kennedy et al. 2013). Conventional pesticides, even those traditionally viewed as benign (Ciarlo et al. 2012), are rendering our crops net sinks for bee populations. These effects are compounded by loss of natural habitat due to landscape simplification, which in itself can result in greater dependency of farms on pesticide inputs due to loss of natural pest suppression (Meehan et al. 2011), which ultimately reduces, or potentially weakens, pollinator pools. Reliability of pollination by wild bees, therefore, relies on judicious use of pesticides and our ability to maintain, or create if necessary, a minimum threshold of natural areas within agricultural matrixes. If landscape level changes are not possible, local efforts such as plantings that boost local bee populations may help wild pollinators overcome the risks associated with pest management. Sound agri-management schemes aimed to sustain wild pollination services will need to balance the benefits of pest management against the costs to wild pollinators, and do so with

the understanding that such trade-offs will change depending on the landscape context (Boreux et al. 2013).

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CHAPTER 3

A REGIONAL ASSESSMENT OF EASTERN APPLE GROWER KNOWLEDGE, PERCEPTIONS, AND ATTITUDES OF NATIVE POLLINATORS

Abstract

Pollinator declines coupled with increasing demand for insect pollinated crops have the potential to cause future pollinator shortages for our most nutritious and valuable crops. Ensuring adequate crop pollination may necessitate a paradigm shift in pollination management, from one that primarily relies on the managed European honey bee (*Apis mellifera* L.) to one that integrates alternative pollinators. While a body of growing scientific evidence supports significant contributions made by naturally occurring wild bees for crop pollination, translating research to practice requires buy-in from growers. Though central to developing agricultural extension and outreach programs that address grower needs and concerns, few studies have assessed grower knowledge, perceptions and attitudes of native pollinators. Here we present findings from sociological surveys of over 600 apple growers in New York State and Pennsylvania, coupled with ecological data from bee surveys. Growers had a general sense of native bee importance, but many were uncertain about wild or alternative managed bee contributions to apple pollination. Despite the uncertainty, a majority of growers demonstrated an openness to relying on wild bees and making low-cost changes to farm management that would benefit wild pollinators. Growers consistently underestimated bee diversity, but their estimates corresponded to major bee groups identifiable by a lay person, indicating accurate local knowledge about wild bees. Grower reliance on honey bees increased with farm size; because wild bee abundance did not measurably decrease with farm size, renting honey bees seemed to be was

motivated by risk rather than grower perception of lower wild bee activity.

Demonstrated effectiveness of wild pollinators and clear guidelines were the most important factors influencing grower decision to actively manage orchards for native bees. Our results highlight a pressing need for an active and research-based extension program to support diversification of pollination strategies in the region.

Introduction

At least, 35% of global food production benefits from-- if not requires-- insect pollinators (Klein et al. 2007). Bees are by far the most important pollinators in agricultural settings, and in terms of ecosystem service, contribute between \$5.7 to \$19 billion per year to the United States economy (Levin 1983, Robinson et al. 1989, Southwick and Southwick 1992, Morse and Calderone 2000) and \$217 billion per year globally (Gallai et al. 2009). Bees support human health by pollinating our most nutritious food crops (Eilers et al. 2011), for which global demands are projected to rise as developing countries become more wealthy (Aizen and Harder 2009). With both domestic and wild bees experiencing global declines (Biesmeijer et al. 2006, Potts et al. 2010, Cameron et al. 2011, van der Zee et al. 2012, Burkle et al. 2013), explicitly incorporating pollinator well-being into farm management decisions may be necessary to ensure sustainable pollination services.

Although more than 20,000 bee species have been described (Ascher and Pickering 2013), pollination management in modern agriculture traditionally involves a single species, the European honey bee, *Apis mellifera* L. Commercially-available and managed honey bees are ideal pollinators in many crop systems, especially in large scale, highly disturbed agroecosystems. Colonies, each producing thousands of foraging workers, can be moved into fields during the flowering period. However, due to steady declines in honey bee populations over the past 50 years (National Research

Council 2007) and significant colony losses due to “Colony Collapse Disorder” (Oldroyd 2007, vanEngelsdorp et al. 2009), it is becoming increasingly risky to rely on a single pollinator species for food production (Winfree 2008). Indeed, if honey bees continue to decline, growers may need to diversify their pollinator portfolio to include alternative pollinators in order to sustain adequate crop pollination in the future.

While developing alternative managed pollinators would diversify pollination strategies, evidence is building for the importance of naturally occurring wild bees for crop pollination. Globally, wild bees are often better pollinators than honey bees (Garibaldi et al. 2013), and the diversity associated with communities of wild bee pollinators stabilizes pollination services spatiotemporally (Kremen et al. 2004, Klein 2009, Garibaldi et al. 2011), in a manner that provides resilience to rapid climate change (Bartomeus et al. 2011, Brittain et al. 2013). Optimizing wild bee pollination services requires a shift in pollination management for growers. In contrast to ordering honey bees for a few weeks, long-term efforts may be required to provide bees with semi-natural or natural areas for food and nesting resources, as well as safety from pesticides beyond the short bloom period (Park et al. in review). Extension education programs will undoubtedly be needed to help growers rely on a suite of pollinators and not just the honey bee (Park, pers. obs). While studies that examine grower knowledge and perceptions of alternative pollinators could inform successful programs that educate and encourage heavier reliance on wild bees, few such studies exist (Partap et al. 2001, Kasina et al. 2009, Munyuli 2011), and even fewer have investigated factors affecting grower pollination strategies (Potts et al. 2011, Hanes et al. 2013).

Here, we surveyed pollination practices, perceptions of wild pollinators and willingness to implement bee-friendly management practices among apple growers in New York (NY) and Pennsylvania (PA). We coupled grower survey data with

ecological bee data to compare perceived with documented importance of wild bees in orchards, to assess grower knowledge gaps, and to guide future extension efforts and management on wild pollination services for apple.

Methods

Study system. Apple (*Malus pumila* Mill: Rosaceae) is an economically important crop in temperate regions of the world, including eastern North America. Apple is self-incompatible and requires cross-pollination by insects (McGregor 1976, Free 1993). While renting honey bees to pollinate this mass blooming crop is commonplace in North America, surveys of orchards over the past century indicate that apple flowers commonly are visited by wild, native bees, particularly species in the genera *Andrena*, *Bombus*, *Halictus*, *Lasioglossum*, and *Osmia* (Hutson 1926, Brittain 1933, 1935, Phillips 1933, Loken 1956, Gardner and Ascher 2006, Park et al. 2010, Watson et al. 2011, Ritz et al. 2012). Recent comparisons reveal that wild bees are equivalent or better pollinators than honey bees on a per-visit basis and contribute important pollination services in orchards when abundant (Park et al. unpublished, Ritz et al. 2012).

New York (NY) and Pennsylvania (PA) are the largest producers of apple in the eastern United States, collectively yielding 1.86 billion pounds of fruit worth \$277 million (USDA NASS, 2009). The apple industry in New York is larger, comprised of over 600 commercial growers (USDA NASS 2011) compared with Pennsylvania's 566 farms (USDA NASS 2008). Though hard to quantify, pollinator extension in PA is more active than in NY, due to the presence of the Center for Pollinator Research at Pennsylvania State University. Native pollinator extension in NY was largely conducted by graduate student M.G. Park from 2010 to 2012, in the form of talks at

grower meetings, a pollinator booklet and a Department of Entomology website (entomology.cornell.edu/wildpollinators).

Grower surveys. Apple growers in NY and PA were surveyed on four major themes: 1) farm and grower characteristics, 2) current pollination strategies, as well as 3) perceptions and 4) attitudes regarding wild and managed alternative pollinators (see Appendix 1 for survey instruments). In New York, Cornell University co-authors contracted the United States Department of Agriculture National Agricultural Statistics Service (USDA NASS) NY field office to administer two mail surveys, one in 2009 and the other in 2012. Surveys were initially conducted by mail with additional respondents contacted by phone until a roughly 50% response rate was achieved. The 2009 survey comprised 16 questions, addressing the four major themes (Park et al. 2010), and served as a base for following surveys. The 2012 survey asked 25 questions, which incorporated additional questions developed by the Pennsylvania team on farm characteristics, the use of managed alternative pollinators and perceived contributions of wild bees to orchard pollination. We also added questions addressing factors important in grower decisions to implement land management practices to benefit native bees and on the effectiveness of a newly released extension booklet on wild pollinators of eastern apple orchards (Park et al. 2012, www.northeastipm.org/park2012 www.), which we included in the survey packet. For several questions asked in 2009, we added more response categories in 2012 from which growers could choose. The surveys were sent to 518 growers in 2009 and 519 growers in 2012. Both had high response rates with 262 (50.6%) and 298 (57.4%) growers completing all or part of the surveys in 2009 and 2012, respectively. Spatially, survey respondents were fairly representative of growers throughout the state as compared to the proportion of growers living within specific counties (USDA NASS 2007, 2012 census data; Table

3.1). Identifying data were not disclosed by USDA NASS to authors in order to ensure respondents' privacy. Unfortunately, targeted surveys of this kind can no longer be conducted by USDA NASS because of privacy concerns over what crops growers produce (Blair Smith, pers. comm.)

In fall 2010, a survey was distributed to PA apple growers with, but a few exceptions, the same 25 questions in the NY surveys. Questionnaires were distributed to fruit growers during extension meetings and other extension events, such as field and plant protection days. The questionnaire was also made available online. A total of 73 growers responded to this survey. Regionally, the pool of respondents for the PA survey was biased to growers from Adams and Lancaster counties and likely reflects the proximity of these growers to the meeting locations where surveys were dispensed. The majority of apple farms are located in Adams County.

Bee surveys. In order to compare grower perceptions of native bees to ecological reality, we included data from bee community surveys conducted at a total 19 farms between 2009 and 2013 in central NY and a total of 9 farms between 2007 and 2013 in PA. In NY, all bees observed visiting apple flowers were net-collected along standardized 15-minutes transects, during peak bee activity with temperatures above 60⁰ F and enough sunlight to cast a shadow (Park et al., in review). Cumulative observed species richness was calculated for each farm across all five years of collecting. In PA, bees were similarly net-collected from visiting apple flowers at different distances, up to 200 m, from the edge. In NY, orchard size and land cover (i.e., natural, agriculture, developed) within a 1 km radius of farms were determined using ArcMap10 GIS (ESRI, 2010). These data are currently unavailable for PA

Table 3.1. County residence of growers who participated in New York and Pennsylvania surveys compared to government censused distributions of apple growers among counties. Data are percentages and only the top 9 counties shown.

New York					Pennsylvania		
2009		2012			2010		
County	survey	census ¹	survey	census ²	County	survey	census ²
Wayne	20.2	16.4	22.6	14.4	Adams	26	7.8
Ulster	10.3	5.7	9.2	5.0	Lancaster	24.7	5.9
Orleans	8.8	6.1	10.1	4.9	York	8.2	4.2
Niagara	6.5	6	6.2	5.0	Bedford	4.1	2.1
Columbia	5	4.1	5.6	2.5	Berks	4.1	4.7
Monroe	3.8	3.1	3.3	2.1	Blair	2.7	0.8
Dutchess	2.7	2.4	2.6	2.7	Lehigh	2.7	1.4
Onondaga	2.7	2.2	3.6	2.0	Northampton	2.7	1.4
Orange	2.3	1.3	3.3	1.7	Snyder	2.7	1.3

¹ 2007 USDA NASS census

² 2012 USDA NASS census

Data analysis. Survey data were summarized using descriptive statistics. To facilitate comparisons among the three surveys, for some questions in the NY 2012 and PA surveys multinomial response variables were collapsed into fewer categories or answers were translated to a common format. For example, PA surveys provided a 5 scale Likert response (*Always, Frequently, Sometimes, Never, Don't Know*) for most questions. Some of these were regrouped into a 3-scale response (*No, Yes, Maybe*) or redefined (e.g., *Very, Moderately, Slightly, Not at all, Don't know*). Chi-square tests were used to compare frequencies of categorical responses between years and states. Univariate analyses were used to compare means of continuous response variables among different levels of categorical factors. Non-parametric Kruskal-Wallis rank sum tests were employed when assumptions of equal variance for ANOVA were not met. We employed generalized linear models (GLM) to explore pre-defined relationships between farm/grower characteristics and perceptions of wild pollinators. Specifically, we predicted that perceived diversity, value of wild bees as pollinators, and openness to relying exclusively on wild pollinators would increase as acres in apple production decreased and would be highest for those farms surrounded by natural areas. These predictions are based on the strong link between healthy wild pollinator communities in fields and proximity to natural areas (Ricketts et al. 2008, Kennedy et al. 2013), and the assumption that growers may be aware of increased wild bee activity in such orchards. To test the effects of farm size, state (NY or PA), and adjacent habitat (collapsed into natural, agricultural and other-mixed) on estimated number of species, we used a negative binomial GLM (Zuur et al. 2013). To test the same effects on whether wild bees were considered valuable for orchard pollination (yes, no, maybe) and whether growers had considered relying exclusively on naturally

occurring native bees (*yes, no, maybe*), we conducted multinomial logistic regressions. Only main effects of size, state and habitat were included and multinomial logistic models were not reduced.

We used descriptive statistics to summarize bee abundance and species richness in each state. Parallel to survey analyses, we investigated effects of size and surrounding natural habitat (at 1 km radius) on wild bee abundance and cumulative observed species richness to see if patterns in the bee data reflected grower perceptions of bee activity and importance in orchards. Size and amount of natural habitat in the landscape were calculated using GIS (ArcMap 10, ESRI). For size, because we followed property boundaries of orchards, we did not account for the fact that some orchards sat adjacent to more orchards, rendering the farm much larger from a bee's perspective. We chose one kilometer because it has been found to be a strong predictive scale for bee response variables (Kremen et al. 2002, Watson et al. 2011). We did not want to go beyond 1km as we wanted land cover to reflect what a grower would consider the farm's surrounding habitat. GLM and generalized linear mixed models (GLMM) were used to analyze diversity and abundance, respectively. In the abundance model, we included farm as a random effect since repeat collecting events occurred within a year, and because of the strong relationship between bee activity and temperature, we included log-transformed temperature as a covariate. Diversity data were pooled at the farm level and, therefore, did not include temperature or a random farm effects.

Statistical models were analyzed in R (R Core Team, 2013); all other analyses were performed in SPSS (IBM Corp, 2013). For general linear models, assumptions of normality and homoscedasticity were met. For negative binomial regressions, we verified that models were not overdispersed (Zuur et al. 2013).

Results and Discussion

Grower and farm characteristics. Table 3.2 summarizes results for questions documenting grower and farm characteristics. NY and PA grower and farm characteristics were similar, but PA growers managed smaller and more diverse farms. While average and range (NY: <1 - 950 ac; PA: <1 – 1200 ac) of apple orchard size in NY and PA were similar, 46% PA growers owned orchards less than 10 acres, compared with 28% and 27% for NY growers in 2009 and 2012, respectively. More PA respondents grew stone fruit ($\chi^2_1 = 39.4, p < 0.001$) and vegetables ($\chi^2_1 = 8.6, p = 0.003$), in addition to apple. Across states, those owning more than 200 acres comprised just a handful of individuals (<10%). Habitat surrounding farms was largely agricultural, forested or mixed, with NY orchards spanning the full spectrum and PA orchards largely split between forested and agricultural landscapes.

Apple production systems in NY and PA have well-established integrated pest management (IPM) programs built over the last 35-40 years (Kovach and Tette 1988, Agnello et al. 2003). This was reflected in the fact that consistently high numbers of apple growers in both states used IPM as their primary pest management strategy. Conventional pest management was used by a maximum 25% growers in NY in 2009. Organic apple production is uncommon in the East due to high rates of disease and pest pressure (Agnello et al. 2003), and in our surveys fewer than 10% of growers had organic orchards. IPM encourages diligent use of pesticides by monitoring pest pressure and spraying only when pest damage causes economic harm. Because it is so widely adopted, IPM may serve as a framework to encourage growers to consider costs to pollinators when making decisions about pesticide applications, and accordingly, current IPM practices may further need to be modified to accommodate pollinators in commercial apple production (Biddinger et al., 2014).

Table 3.2. Grower and farm characteristics, New York (2009 and 2012) and Pennsylvania (2010) apple. SEM provided with means in parentheses. Blanks indicate the questions or specific responses were not included in surveys.

Grower and farm characteristics	New York				Pennsylvania	
	2009		2012		2010	
	<i>N</i>	Mean	<i>N</i>	Mean	<i>N</i>	Mean
Acreage in apple production	262	79.5 (7.8)	298	80.2 (7.5)	73	96.6 (24.4)
Number apple varieties	262	15.5 (0.7)	298	17.6 (1.0)	73	21.5 (3.7)
		Percent		Percent		Percent
Percent income derived from apple			296			
0-25				35.5		
25-50				12.8		
50-75				23		
75-100				28.7		
Primary habitat surrounding orchard	262		296		73	
Orchard		8.5		5.7		11
Suburban		8.9		8.0		9.6
Forest		18.9		24.3		39.7
Meadow		4.6		3.3		0
Agricultural		37.5		37.3		39.7
Mixed		21.6		21.3		0
Pest management style	249		296		73	
Conventional		24.9		18.5		16.4
IPM		64.3		70		79.5
Organic		8.4		5.4		1.4
Other		2.4		6.1		0
Grow other stone fruits			298		72	
Yes				54.5		93.2
No				45.5		5.5
Grow vegetable crops			298		72	
Yes				42		60.3
No				58.1		38.4

From the 2012 NY survey, we found that percent of total income gained from apple was distributed evenly among three collapsed categories: 0-25, 25-75, 75-100 %, and increased significantly with orchard size ($\chi^2_3 = 164.6$, $p < 0.0001$; Fig. 3.1).

Pollination strategies. Table 3.3 summarizes results for questions documenting current pollination strategies. Roughly 50% of NY and PA growers reported renting honey bees ($\chi^2_1 = 2.1$, $p = 0.2$) for apple pollination, but the probability of renting bees depended directly on orchard size ($\chi^2_1 = 11.8$, $p = 0.001$, Fig. 3.2), a pattern consistent in both states (state \times acre: $\chi^2_1 = 2.7$, $p = 0.1$). PA and NY growers stocked honey bees in orchards at similar densities (NY: 2.5 ± 0.4 hives/ac, $n = 181$; PA: 1.9 ± 0.2 hives/ac, $n = 44$; $t_{223} = 0.752$, $p = 0.5$) and paid similar prices per hive (NY: $\$63.90 \pm 2.8$; PA: $\$59.30 \pm 4.40$; $t_{151} = 0.631$, $p = 0.5$). In NY, regardless of orchard size, the majority of growers considered honey bee rentals a minor to moderate expense. Similar results were found for PA growers with less than 100 acres; however, growers with 100-500 acres in apple described honey bee rentals to be a major expense (within PA, $\chi^2_{15} = 26.6$, $p = 0.03$). These results suggest that hive prices have not yet inflated to the point where growers would be motivated to invest in other pollinator strategies, except for a small subset of large PA growers.

Grower adoption of alternative managed pollinators was not trivial in terms of buying commercial bumble bees; however, the use of mason bees was low. In NY and PA, 16.7% and 24.3% growers, respectively, reported using bumble bees, at least, sometimes. Few growers reported having used commercial mason bees for apple pollination, with a study-wide maximum of 8% growers in PA. Though not statistically significant, familiarity of mason bees as alternative pollinators increased in NY by the second survey, which may translate to higher adoption in the future. Bumble bees are known to be reliable pollinators because they forage in cooler

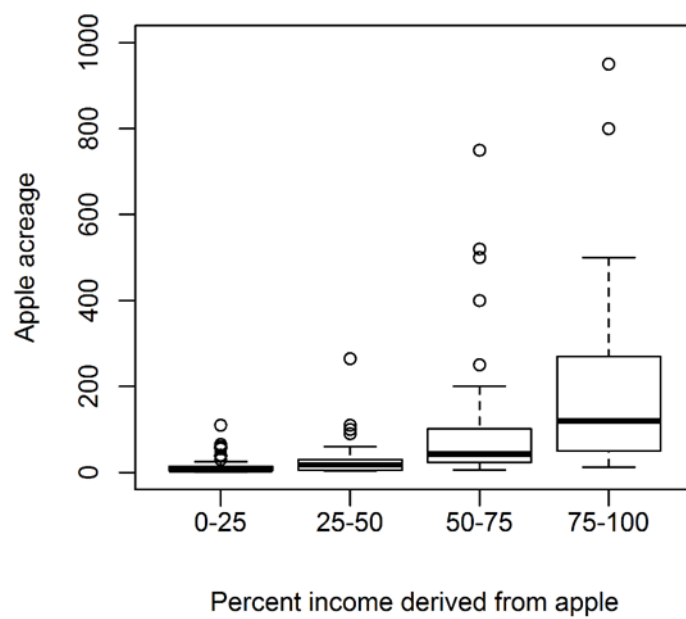


Figure 3.1. Correlation between financial reliance on apple production and apple acreage owned by growers.

Table 3.3. Pollination strategies among New York and Pennsylvania apple growers. Blanks indicate the questions or specific responses were not included in surveys.

Pollination strategy	New York				Pennsylvania	
	2009		2012		2010	
	N	%	N	%	N	%
Rent honey bees	257		297		73	
Yes		60.7		53.5		49.3
No		39.3		46.5		50.7
Expense of honey bee rentals	223		160		67	
Major		25.11		14.4		8.2
Moderate				33.1		24.6
Minor		74.89		49.4		60.3
No opinion				3.1		4.1
Familiar with mason bees	253		297			
Yes		29.4		42.5		
No		64.3		57.5		
Maybe		6.3				
Use commercial mason bees	253		297		72	
Yes		2		2.7		9.6
No		97.2		97.3		89
Maybe		0.8				1.4
Use commercial bumblebees			297		72	
Always				4.0		4.1
Frequently				2.3		4.1
Sometimes				9.3		13.7
Never				83.3		76.7
Don't know				1.0		1.4
Consider impacts of pesticides	249		295		72	
Yes		93.2		97.3		97.3
No		4.8		2.0		1.4
Sometimes		2		0.7		5.0
CCD threatens apple production	247		297		71	
Yes		59.1		56.7		73.2
No		19.4		10.3		15.5
Maybe /Don't know		21.5		33.0		11.3
Pollination limited by pollinator availability	249		297		71	
Yes		36.1		52.3		47.9
No		41		29.2		43.7
Maybe		22.9		18.5		8.5

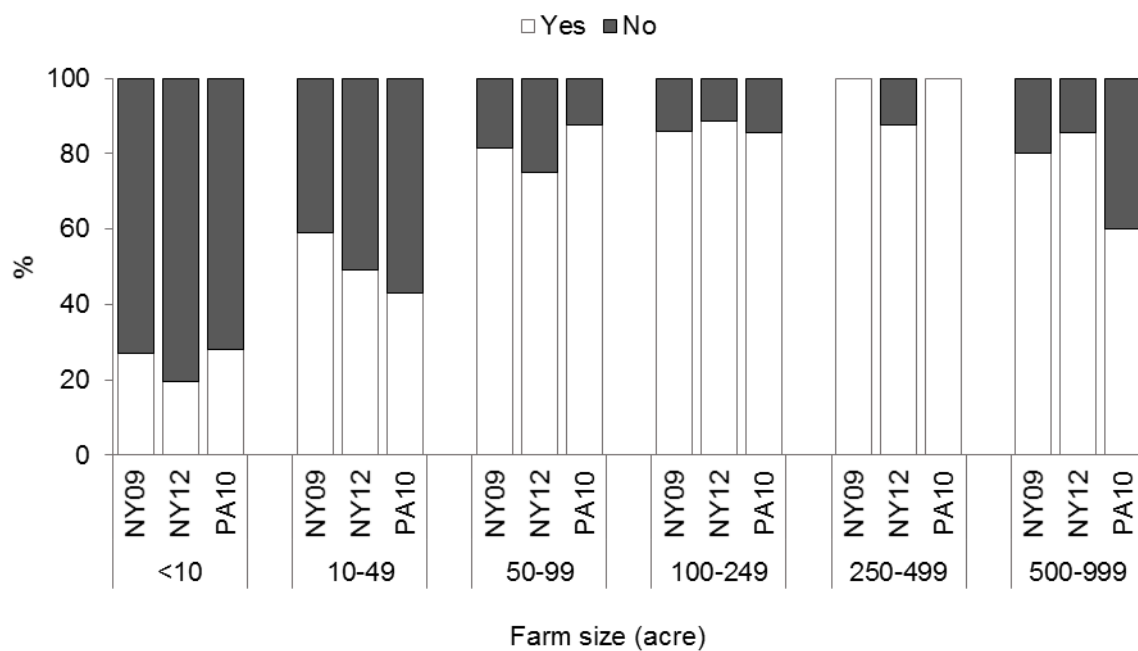


Figure 3.2. Proportion of apple growers in New York (NY) and Pennsylvania (PA) that reported renting honey bees for pollination increased with farm size.

temperatures than honey bees, but are expensive. While native blue orchard bees (*Osmia lignaria*) are rarely collected and do not establish well in NY (R. Williams, pers. comm.), the introduced horn-faced bee, *O. cornifrons*, has established throughout the east coast, and there is interest in further developing *O. cornifrons* as an alternative managed pollinator in our study region.

Concern over reliable pollination was high among all growers. Study-wide, between 36% and 52% growers reported having experienced limited apple pollination due to inadequate availability of pollinators. Several growers commented that bad weather was an important driver of low bee activity. A particularly wet spring in 2011 and cold spring in 2012 may have contributed to higher reports of pollination limitation in 2012 as compared with 2009 in NY. Providing a Likert scale of response options (i.e., *always, frequently, sometimes, never, don't know*) in the two most recent surveys, revealed that for the majority of growers pollinator limitation occurred only sometimes. Recent declines in honeybee populations due to CCD were considered a threat to successful apple production by the majority of apple growers surveyed, but a sizeable proportion of growers in NY also were unsure about the impacts of CCD. While not statistically different ($p > 0.05$), lower uncertainty about impacts of CCD among PA growers may reflect greater exposure to extension efforts and resources on pollinator health through Penn State's Center for Pollination Research, Native Bee Research Program of the Fruit Research and Extension Center and/or reflect a biased pool of extension meeting attendees, who may be inherently more interested in staying abreast of the latest news and research. These documented concerns echo those found among blueberry growers in Maine (Hanes et al. 2013).

Regardless of year and state, almost all (> 93%) surveyed growers reported that they already considered pollinator safety when applying pesticides in orchards. In both states, apple is an intensively sprayed fruit crop given intense pest and disease

pressure (Agnello et al. 2009); applied insecticides and fungicides have been shown to impact wild pollinators in our study system (Park et al. in review), and some orchard pesticides used in this region have been reported toxic to orchard pollinators (Biddinger et al. 2013b). Aside from intrinsic motivations to protect pollinators, growers have many practical reasons to be cognizant of pollinators when considering their pest management options: 1) adequate fruit set for crop production depends on adequate pollination; 2) many growers pay to have bees in the orchard so harm to bees would be counterproductive; and 3) label guidelines restrict use of insecticides during bloom when bees are most active in orchards. High appreciation of native pollinators was also observed among blueberry (Hanes et al. 2013) and cranberry growers (Gaines & Gratton, unpublished).

Perceptions and attitudes of wild bees. Grower estimates of bee species diversity were low, especially among NY growers, but accurately reflected easily identifiable morphological groups. We observed 100 bee species in NY and 52 bee species in PA visiting apple flowers study-wide. At the farm level, observed species richness ranged from 15-51 in NY. On average, growers in PA and NY estimated 30.1 ± 4.0 and 17.3 ± 1.1 native bee species visiting apple in their state, respectively ($t_{402} = -3.1$, $p < 0.001$). In spite of extension efforts on native pollinator diversity in NY, grower diversity estimates only marginally increased between 2009 and 2012 (15.4 v. 19.7 species; $t_{336} = -1.89$, $p = 0.06$). Observed species richness in NY was significantly and positively influenced by the amount of natural area surrounding farms but not by orchard size (Table 3.4). In contrast, grower estimates of bee diversity were not affected by habitat type or farm size (Table 3.5). PA growers had greater knowledge of bee species diversity in their farms, which again could be attributed to a biased pool

Table 3.4. Effects of orchard size, percent natural areas within 1km and ln-transformed temperature on wild female bee abundance (GLMM), and effects of orchard size and percent natural areas on total observed wild bee species richness (GLM) in New York State. Temperature was ln(x) transformed and abundance was ln(y+1) transformed. All predictors but year were mean centered. Coefficients are not back-transformed. ‘-’ indicates the predictor was not included in the full model. Full factorial models included orchard size and were reduced through backwards stepwise selection. Because orchard size was never a significant predictor of bee abundance or diversity, we excluded it from the table.

Effect	Abundance			Diversity		
	Coeff (SEM)	<i>d.f.</i>	<i>p</i> -value	Coeff (SEM)	<i>d.f.</i>	<i>p</i> -value
Natural area	0.018 (0.0062)	17	0.0085	0.45 (0.16)	17	0.013
Temperature	1.16 (0.22)	165	<0.0001	-	-	-
Year	-0.66 (0.072)	165	<0.0001	-	-	-

Table 3.5. Effects of state, orchard size, and habitat adjacent to orchards on 1) grower estimates of native pollinator diversity in apple orchards, 2) whether growers considered native bees valuable to apple pollination, and 3) whether growers had considered relying exclusively on wild bees. Habitat categories were collapsed into agriculture, natural and other. “Other” included mixed and suburban habitats. For estimates of bee diversity, a negative binomial GLM was employed and reduced via backwards stepwise regression. Predictors that were not significant (at $\alpha = 0.05$) but contributed significantly to model fit were retained. Multinomial logistic regressions were conducted on response variables with three levels: yes, no and maybe and were not reduced. Coefficients in multinomial logistic regression are log odds ratios. Significant effects are bolded.

Table 3.5

Effect	Coeff (SEM)	z	p-value
<i>Estimated bee species richness (d.f. = 540)</i>			
State (ref = NY)	0.57 (0.00032)	4.48	< 0.0001
Orchard size (ac)	-0.00020 (0.00032)	-0.63	0.5
Habitat (ref = Natural)			
Agricultural	-0.12 (0.11)	-1.11	0.3
Other/Mixed	-0.17 (0.12)	-1.36	0.2
<i>Wild bees are valuable pollinators (N = 628, ref = No)</i>			
State (ref = NY)			
Yes	0.53 (1.05)	0.50	0.6
Maybe	0.48 (1.13)	0.42	0.6
Orchard size (ac)			
Yes	0.00061 (0.002)	0.28	0.78
Maybe	0.0014 (0.002)	0.61	0.54
Habitat (ref = Natural)			
Agricultural			
Yes	0.11 (0.66)	0.17	0.87
Maybe	-0.025 (0.72)	-0.034	0.97
Other/Mixed			
Yes	-0.30 (0.66)	-0.45	0.65
Maybe	-1.24 (0.79)	-1.57	0.54
<i>Considered relying exclusively on wild pollinators (N = 620, ref = No)</i>			
State (ref = NY)			
Yes	0.63 (0.31)	2.04	0.04
Maybe	-0.14 (0.79)	-0.18	0.86
Orchard size (ac)			
Yes	-0.0040 (0.00077)	-5.18	<0.0001
Maybe	-0.0012 (0.0014)	-0.84	0.04
Habitat (ref = Natural)			
Agricultural			
Yes	-0.65 (0.22)	-2.94	0.0033
Maybe	-1.16 (0.48)	-2.40	0.017
Other/Mixed			
Yes	-0.17 (0.25)	-0.68	0.49
Maybe	-0.51 (0.51)	-1.01	0.31

of growers who attend extension meetings or to more active extension programs in PA on alternative pollinators.

The fact that growers with orchards surrounded by forest did not report higher bee diversity estimates than those with orchards in simplified landscapes, suggests a lack of awareness among growers of the types of native pollinators visiting orchards. Alternatively, growers may be highly aware but low species estimates reflected a lay person's ability to identify bees based on easily recognizable morphological groups. Bee species are commonly distinguished by characteristics only visible under a microscope, making it challenging to differentiate species in the field. For this reason, wild bees are commonly lumped into morphological groups (e.g., "metallic green bee") to facilitate observations of bee visitation by lay persons. Following "Pennsylvania Citizen Scientist Pollinator Guide" (Donovall and vanEngelsdorp 2008), apple bees in PA and NY could be lumped into 12 distinct morphological groups, which mirrored median grower diversity estimates of 10 species. Additionally, a given orchard will support a subset of bee species found study-wide, so the lower species count may also reflect local knowledge. Thus grower perceptions of bee diversity accurately reflect a lay person's ability to distinguish among bee groups, but also indicate a knowledge gap about the sheer diversity of native bees.

Almost all growers thought native bees were valuable for apple pollination; however, growers expressed uncertainty when asked to quantify the contributions of wild bees to pollination. Native bees were viewed by 85 – 93% surveyed growers as valuable pollinators in apple orchards; this high appreciation did not change with farm characteristics or state (Table 3.5). Providing growers with a Likert scale in 2012 NY and PA surveys, we found that 50% of growers rated native bees with the highest value ranking: always (PA) or very important (NY), but that 6-10% of growers reported not knowing the value of native bees for their apple orchard. For 2012 NY

and PA surveys, we asked growers to estimate the contribution of native bees to apple pollination in their orchards. As a group, growers estimated $45 \pm 1.6\%$ (NY) and $51 \pm 3.5\%$ (PA) of orchard pollination was due to native bees ($t_{300} = -1.6$, $p = 0.1$), but individual estimates ranged widely and 20% expressed that they did not know (available answer in the NY 2012 survey only). Similarly, when asked whether alternative managed pollinators, such as mason or bumble bees, were important for apple pollination (PA-only question), 68% were evenly split among alternative managed pollinators being always, frequently or sometimes important, 6% reported they were never important, and 29% reported that they did not know. Grower uncertainty in the effectiveness and importance of native or wild pollinators is understandable given such information has only recently been quantified (Blitzer et al., unpublished, Park et al., unpublished, Ritz et al. 2012, Garibaldi et al., 2013; Biddinger et al. 2013a). These recent studies have used different methods but consistently found wild bees to be as effective if not more so than honey bees for apple pollination. Additionally, relative contributions of wild bees at the orchard level depend directly on their abundance, which fluctuates from farm to farm as a function of the surrounding habitat and pesticide use (Park et al., in review).

Whether a grower had considered relying exclusively on wild pollinators was most influenced by farm size (Fig. 3.3), but also depended on state and habitat around farms (Table 3.5). As acreage in apple production increased, so did the ratio of growers who had never considered relying exclusively on wild native bees; however, even among the largest apple operations a third of growers had considered foregoing honey bee rentals. Higher proportion of PA growers had considered relying on wild bees than NY growers. Higher proportions of growers with orchards surrounded by agriculture did not consider relying on wild bees compared with growers whose orchards were near natural or mixed/suburban areas. While observed bee diversity and

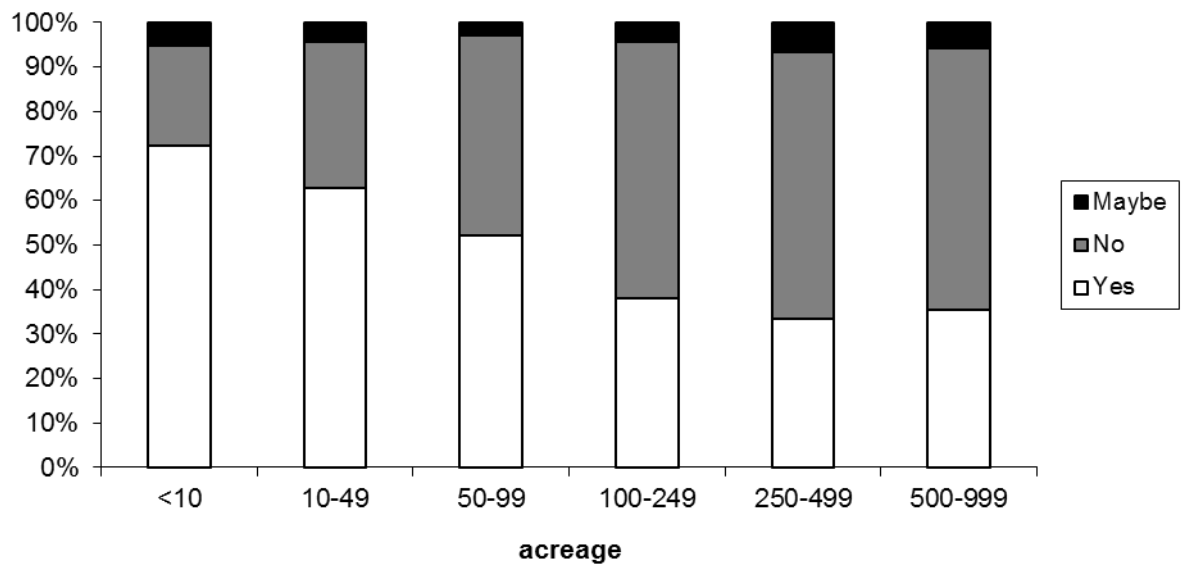


Figure 3.3. Frequencies of grower response to whether they had ever considered relying exclusively on native pollinators changed with acres in apple production. New York and Pennsylvania grower data pooled as no difference as found between states ($\chi^2_2 = 4.31, p = 0.1$).

bee abundance did not change with farm size, the amount of natural area within 1km had a strong positive influence on both (Table 3.4). We speculate, therefore, that decreasing openness to relying on wild pollinators with increasing size is motivated by an aversion to risk rather than an awareness that there may be fewer native bees in larger apple orchards to provide adequate pollination services. Farm size and percent total income derived from apple production were highly correlated (Fig. 3.2). Understandably, growers who rely more heavily on apple for a source of income may be less willing to risk inadequate pollination and, therefore, always rent honey bees. In regards to the influence of habitat, grower attitudes about relying on native bees were congruent with the ecological data; suggesting that growers may have a sense of increased wild pollinator activity in orchards near natural habitat. Overall, growers demonstrated a surprising openness to relying exclusively on native pollinators.

To gauge willingness of growers to enhance wild pollination, we asked if they would consider low-cost land management practices that would increase native bees in their orchard. Consistent across surveys, a majority of growers indicated they would consider such action, with 85% PA growers being willing compared with 50-68% NY growers. Growers were also asked about their knowledge of and participation in federal cost-share programs, designed to aid grower efforts to create or maintain pollinator habitat. The Food, Conservation, and Energy Act of 2008 created federal government funding to conserve and protect pollinators in agricultural ecosystems. As a result, growers in this region or elsewhere in the United States were encouraged to adopt pollinator-friendly production practices (for instance, creating pollinator habitat or strip in the farm by planting different flowering plants that pollinator visits) and were rewarded incentives (by the government) upon implementing such practices (Vaughan et al., 2012a; Vaughan et al., 2012b). In NY and PA, most native bees are pollen bees, and presence of mixture floral resources around farms could be very

important in conserving and maintaining healthy population of these bees. 91% and 75% of NY and PA growers, respectively, reported not knowing about federal cost-share programs, and of those who did, only 8% of NY and 16% PA growers were enrolled. Thus, PA and NY growers seemed generally open to the idea of relying more on native pollinators; however, many growers – especially in NY-- were not aware of the resources available to them to enhance wild bee habitat in their orchards.

To identify obstacles that prevent growers from actively enhancing wild pollinator populations in orchards, we asked growers to rank the importance of several factors (from *not at all important* to *very important*) that would influence their decision to implement land management changes for wild bees (Fig. 3.4). Of the top three factors, proven effectiveness of wild pollinators was most important, clear guidelines to implement management practices was second, and environmental stewardship was third. Evidence for the effectiveness of wild pollinators for apple production has recently been demonstrated empirically (Blitzer et al. unpublished, Ritz et al. 2012, Park et al unpublished), but the level of pollination provided by wild bees depends directly on their abundance, which varies across farms and among years (Park et al. in review). In order for growers to assess wild pollination services available in orchards, accessible protocols to monitor native bee populations need to be developed (Hanes et al. 2013). The importance of clear guidelines stresses the critical role extension programs will play in helping growers adopt new pollination management practices. For example, creating new habitat may require growers to plant floral species with which they are unfamiliar, and negotiating the unknowns without technical support can be difficult. On-sight assessments of grower needs to create additional habitat will be important, as many growers may have adequate natural areas but could consider avoidance strategies, such as spraying at night when bees are inactive. Grower opinion that cost was not the most important consideration when

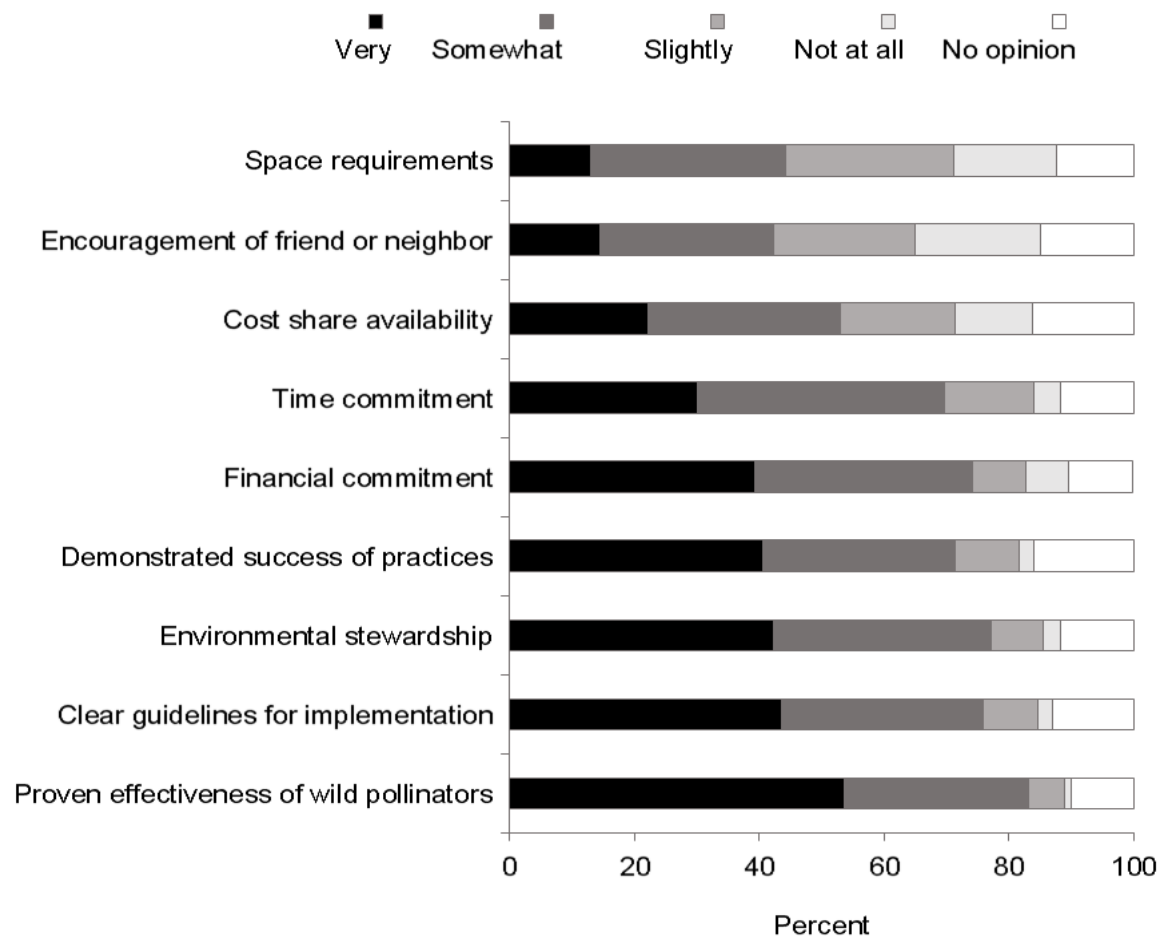


Figure 3.4. Importance of factors grower decision to adopt new land management practices to protect or enhance wild pollinators.

deciding to implement land management practices for wild bees and resistance to government financial aid could contribute to a lack of interest in government cost share programs. Pollinator habitat creation at the landscape scale has been forwarded as a means by which society can increase food sustainability, by enhancing wild pollination services for crops, and can conserve diversity in agricultural landscapes (Potts et al. 2011). For such a coordinated vision to become a reality, much more outreach and extension support on crop pollination is needed (Hanes et al. 2013).

Pollinator booklet assessment. In order to assess the effectiveness of a new extension booklet on wild pollinators of eastern apple, we asked growers to rank the degree to which they agreed with statements related to 1) learning outcomes and 2) change in reader attitudes or behavior. The booklet was highly successful in terms of the prescribed learning outcomes and moderately influential in terms of encouraging readers to engage in activities that will enhance wild pollinator conservation on their farm (Fig. 3.5). These results suggest that information in print is a viable means of conducting outreach to apple growers. The widespread distribution of the booklet on the East coast (10,000 to date) suggests a need for more extension materials on wild pollination that cater recommendations to regional audiences.

Conclusions

Integrating biological and grower survey data allowed us to explore grower awareness of pollinators as well as factors influencing grower perceptions. We found overwhelming support among eastern apple growers for the importance of wild pollinators and native bees, an openness to rely more on naturally occurring bees, and willingness to make low-cost changes to enhancing wild bee populations. At the same time, we documented sizeable uncertainty among growers about the effectiveness of

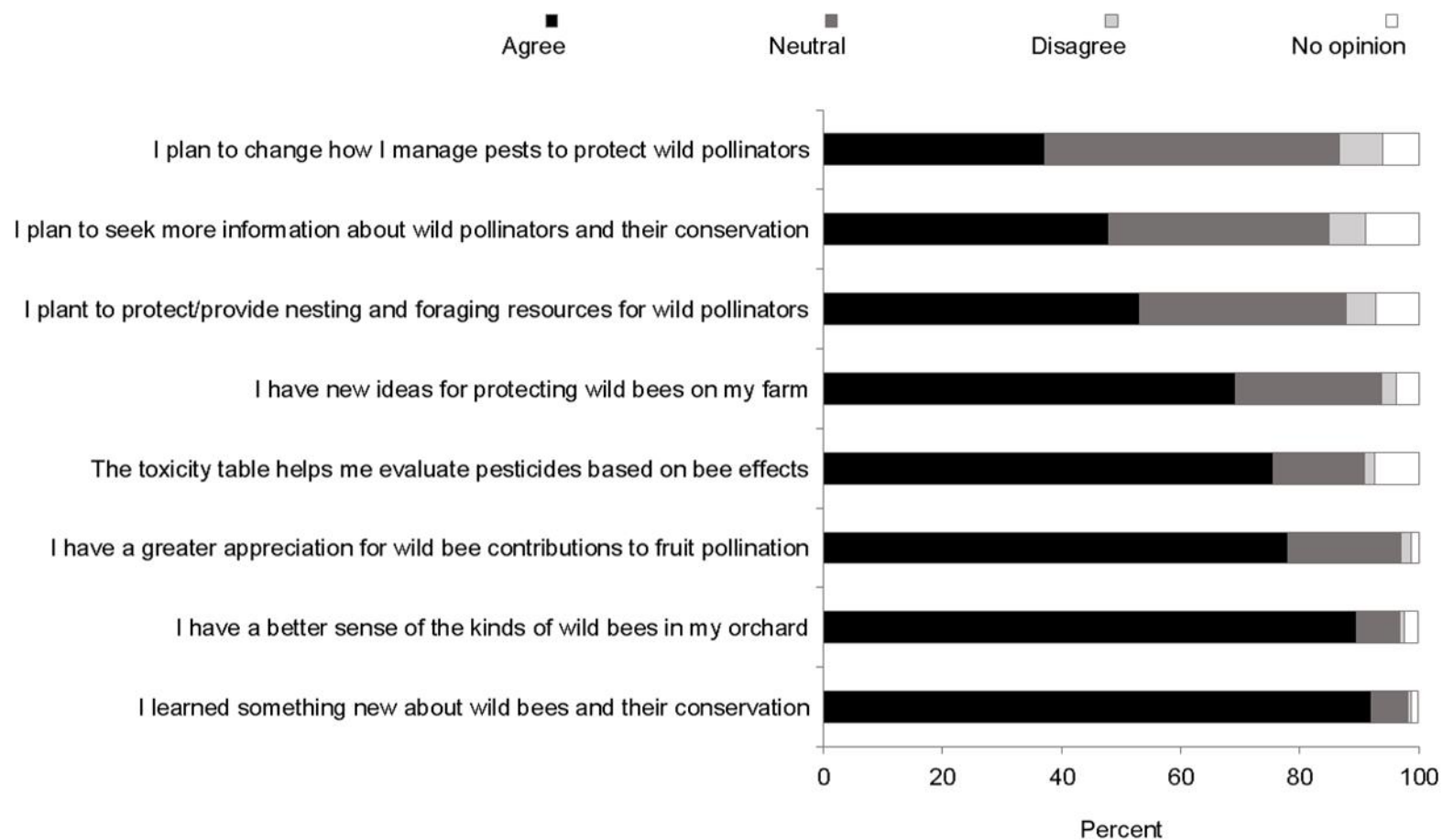


Figure 3.5. Grower learning outcomes and attitudes from reading the extension booklet, “Wild pollinators of eastern apple orchards and how to conserve them.”

wild and alternative managed bees for apple pollination, as well as a tendency to rent honey bees to reduce the risk of crop loss. This uncertainty was the largest obstacle reported by growers to actively manage orchards to protect wild pollinators. Evidence for the effectiveness of wild pollinators has grown in our study region, and world-wide. This is a perfect time to take the scientific evidence and encourage growers to consider wild pollinators as part of their pollination strategy. By no means do we advocate that growers abandon the use of honey bees altogether, but a more integrated pollination management approach seems viable in our study region and may ensure growers continue to receive optimum pollination in the face of volatile honey bee supplies. Proactive steps to support wild pollinators on farms will equally benefit honey bees as well. With a strong history of IPM in the region, extension programs provide an existing infrastructure in which to develop technical and informational support to ensure sustainable food production systems that rely on insect pollination, like apple.

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APPENDIX 1: SURVEY INSTRUMENTS



NATIONAL
AGRICULTURAL
STATISTICS
SERVICE

**New York Agricultural Statistics
Service**

Dept. of Agriculture & Markets
10B Airline Drive
Albany, NY 12235
518-457-5570
1-800-821-1276
Fax: 1-800-591-3834



Cornell University

APPLE POLLINATION SURVEY 2009

1. How many total acres do you have in apple cultivation?
Acres

2. How many apple varieties do you grow?
Varieties

For Questions 3-16, please circle your answer

3. What is the primary habitat surrounding your orchard?
Orchard Suburban Forest Meadow Agricultural Other

4. Do you rent honey bees for apple pollination?
Never Sometimes Always

5. Do you view honey bee colonies as a major or minor expense?
Major Minor

6. What would you estimate to be the number of native bee species that visit
apple blossoms in New York State?
1 10 30 40 100

7. Do you view native bees (*honey bees are not native*) as valuable pollinators
in your apple orchard?
Yes No Maybe

8. Would you be surprised if native bees were important pollinators of apple trees in New York State?
Yes No Maybe
9. Are you familiar with alternative managed apple pollinators such as orchard mason bees (*genus Osmia*)?
Yes No Maybe
10. Have you ever used commercially available orchard mason bees, such as the blue orchard mason bee (*Osmia lignaria*), for apple pollination?
Yes No Maybe
11. Have you ever considered relying entirely on the natural occurring native bees for pollination of apples?
Yes No Maybe
12. How would you describe your management practices regarding pesticides, herbicides, fungicides, etc.?
Conventional Integrated pest management (IPM) Organic Other: (*please indicate*)
13. If/when you use chemical treatments, do you take into consideration the impact on pollinators?
Yes No Sometimes
14. Would you consider adopting (*low-cost*) land management practices that would increase the diversity and abundance of native bees in and around your farm?
Yes No Maybe (*please elaborate*) _____
15. Do you view recent declines in honey bee populations due to colony collapse disorder (CCD) a threat to successful apple production?
Yes No Maybe
16. In your experience, is successful apple pollination limited by the availability and/or abundance of bees (*e.g., have you ever experienced poor fruit set because of a shortage of native or managed bees*)?
Yes No Maybe

Mid-Atlantic Apple Pollination Survey 2010

D. Biddinger & E. Rajotte, Penn State University

Adapted from a Cornell University Survey by Mia Park

1. If you use honey bees for apple pollination, what is the average number of hives used on a per acre basis or indicate if less than 1/acre?...../Acre or 1 per acres
2. If you rented honey bees for pollination in 2010, how much did you pay per hive?.....\$
3. What percentage of apple pollination on your farm do you consider is being provided by bees other than honey bees?%
4. What would you estimate to be the number of native bee species that visit apple blossoms in Pennsylvania? (circle one answer)
1 10 50 100 200 300

For Questions 5-25, please circle one answer

5. What is the primary habitat surrounding your orchards?
Orchards Suburban Forest Meadow Agricultural Other
6. Do you rent honey bees for apple pollination?
Never Sometimes Frequently Always Don't Know
7. Do you consider honey bee colonies as a major expense on your farm?
Never Sometimes Frequently Always Don't Know
8. Native bees (*honey bees are not native*) are valuable pollinators in your apple orchard?
Never Sometimes Frequently Always Don't Know

9. Alternative managed apple pollinators such as orchard mason bees (*genus Osmia*) can be important in PA apple orchards.

Never Sometimes Frequently Always Don't Know

10. Have you ever used commercially available bumble bees for apple pollination?

Never Sometimes Frequently Always Don't Know

11. Have you ever used commercially available orchard mason bees, such as the blue orchard mason bee (*Osmia lignaria*) or the Japanese Orchard bee (*Osmia cornifrons*) for apple pollination?

Never Sometimes Frequently Always Don't Know

12. Have you ever considered relying entirely on the natural occurring native bees for pollination of apples?

Never Sometimes Frequently Always Don't Know

13. If/when you use insecticide treatments, do you take into consideration the impact on pollinators?

Never Sometimes Frequently Always Don't Know

14. Would you consider adopting (*low-cost*) land management practices that would increase the diversity and abundance of native bees in and around your farm?

Never Sometimes Frequently Always Don't Know

15. Do you consider recent declines in honey bee populations due to colony collapse disorder (CCD) a threat to successful apple production in your orchards?

Never Sometimes Frequently Always Don't Know

16. In your experience, is successful apple pollination limited by the availability and/or abundance of bees (*e.g., have you ever experienced poor fruit set because of a shortage of native or managed bees*)?

Never Sometimes Frequently Always Don't Know

17. How would you describe your management practices regarding pesticides, herbicides, fungicides, etc.?

Conventional Integrated Pest Management (IPM) Organic Other:
(*please indicate*)

18. Are you aware that USDA Natural Resources Conservation Service will cost share pollinator habitat creation and maintenance?

Yes No

19. Is any part of your apple crop enrolled in this NRCS pollinator habitat program?

Yes No

20. What state is your farm in?

21. How many total acres do you have in apple cultivation?

.....

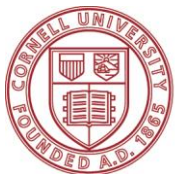
22. Do you also grow stones fruits (i.e. cherry, peach/nectarines and plums)?

Yes or No

23. Do you also grow vegetable crops? Yes or No

24. How many apple varieties do you grow?

25. What county is the majority of your orchard in?



Cornell University

Apple Pollination Survey 2012

1. How many total acres do you have in apple cultivation? _____ Acres

2. How many apple varieties do you grow? _____ Varieties

For the following questions please check one response only.

3. What percent of your **total** income is derived from apple production?

☐ 0-25% ☐ 25-50% ☐ 50-75% ☐ 75-100%

4. Do you also grow stone fruits (i.e., cherry, peach/nectarines and plums)? ☐ Yes ☐ No

5. Do you also grow vegetable crops? ☐ Yes ☐ No

6. What is the primary habitat surrounding your orchard?

☐ Orchard ☐ Suburban ☐ Forest ☐ Meadow ☐ Agricultural ☐ Other: _____

7. Do you rely on (e.g., rent, borrow, use neighbor's) honey bees for apple pollination?

☐ Always ☐ Frequently ☐ Sometimes ☐ Never ☐ Don't Know

If you rely on honey bees, what is the average number of hives used on a per acre basis? _____/ acre

8. Do you RENT honey bee colonies? ☐ Yes ☐ No

IF YES, how much did you pay per hive in 2012? \$ _____

IF YES, how do you view this expense for your apple production?

☐ Major ☐ Moderate ☐ Minor ☐ No opinion

9. What would you estimate to be the number of native bee species that visit apple blossoms in New York State?

☐ 1 ☐ 10 ☐ 30 ☐ 40 ☐ 100 ☐ Don't know

10. How valuable do you view native bees (honey bees are not native) as pollinators in your apple orchard?

☐ Very ☐ Moderately ☐ Slightly ☐ Not at all ☐ Don't know

11. What proportion of apple pollination on your farm do you believe is provided by bees other than honey bees?

☐ 0-25% ☐ 25-50% ☐ 50-75% ☐ 75-100% ☐ Don't Know

12. Have you ever considered relying entirely on natural occurring native bees for pollination of apples?

☐ Always ☐ Frequently ☐ Sometimes ☐ Never ☐ Don't Know

13. Have you ever used commercially available bumble bees for apple pollination?

☐ Always ☐ Frequently ☐ Sometimes ☐ Never ☐ Don't Know

14. Besides bumble bees, are you familiar with other alternative managed apple pollinators, such as orchard mason bees (genus *Osmia*)? ☐ Yes ☐ No

15. Have you ever used commercially available orchard mason bees, such as the Blue Orchard bee (*Osmia lignaria*) or the Hornfaced bee (*O. cornifrons*), for apple pollination? ☐ Yes ☐ No

16. How would you describe your management practices regarding pesticides, herbicides, and fungicides?

☐ Conventional ☐ Integrated pest management (IPM) ☐ Organic ☐ Other: _____

17. If/when you use chemical treatments, do you take into consideration the impact on pollinators?

☐ Always ☐ Frequently ☐ Sometimes ☐ Never ☐ Don't Know

18. Do you view recent declines in honey bee populations due to colony collapse disorder (CCD) a threat to successful apple production?

☐ Yes ☐ No ☐ Maybe/Don't Know

19. In your experience, is successful apple pollination limited by the availability and/or abundance of bees (e.g., have you ever experienced poor fruit set because of a shortage of native or managed bees)?

☐ Always ☐ Frequently ☐ Sometimes ☐ Never ☐ Don't Know

20. Would you consider adopting (low-cost) land management practices that would increase the diversity and abundance of native bees in and around your farm? ☐ Yes ☐ No ☐ Maybe

21. Before receiving the booklet, "Wild pollinators of eastern apple orchards and how to conserve them," were you aware that USDA Natural Resources Conservation Service provides cost share programs to create and maintain pollinator habitat on your farm? ☐ Yes ☐ No

IF YES, is any part of your apple crop enrolled in this NRCS pollinator habitat program? ☐ Yes ☐ No

22. How **important** are each of the following factors in your decision to adopt new land management practices to protect or enhance wild pollinators? (Check one reply per factor)

	Very	Somewhat	Slightly	Not at all	No opinion
a. Financial commitment.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
b. Time commitment.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
c. Space requirements.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
d. Availability of cost share programs.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
e. Demonstrated success of management practices.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
f. Environmental stewardship.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
g. Encouragement of friend or neighbor.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
h. Proven effectiveness of wild bees as pollinators.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
i. Clear guidelines to implement management practices...	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
j. Other:_____					

The next questions refer to the accompanying booklet, “Wild pollinators of eastern apple orchards and how to conserve them”. Please answer them only after you have had a chance to review the booklet.

23. Have you read the accompanying booklet? ☐ Yes ☐ No

IF NO, then your survey is complete.

24. After reading the booklet, do you **agree** with the following statements? (Check one reply per statement)

	Agree	Neutral	Disagree	No opinion
a. I learned something new about wild bees and their conservation.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
b. I have a better sense of the kinds of wild bees in my orchard.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
c. I have greater appreciation for the contribution of wild bees to fruit pollination.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
d. The toxicity table makes it easier for me to evaluate my pesticide options based on their effects on bees.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
e. I have new ideas of how to protect wild pollinators on my farm....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

25. After reading the booklet, do you **agree** with the following statements? (Check one reply per statement)

	Agree	Neutral	Disagree	No opinion
a. I plan to change the way I manage pests in my orchard to protect wild pollinators (e.g., timing of sprays).....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
b. I plan to protect or provide nesting and foraging resources for wild pollinators.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
c. I plan to seek additional information about wild pollinators and their conservation.....	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>